



Half a century of citizen science tag-recapture data reveals stock delineation and cross-jurisdictional connectivity of an iconic pelagic fish

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Abstract Tag-recapture programs to monitor the movements of fish populations are among some of the longest-running citizen-science datasets to date. Here, using half a century of yellowtail kingfish (*Seriola lalandi*, Carangidae) tag-recapture data collected through citizen-science projects, we report novel insights into population connectivity in Australia and New Zealand (NZ). Despite the importance of kingfish in commercial and recreational fisheries,

substantial knowledge gaps about their stock structure and connectivity between jurisdictions hinder current management efforts. Between 1974 and 2022, 63,432 releases and 4636 recaptures (7.3%) of tagged kingfish were collected in Australia and NZ. Most tagged individuals (51.4%) were recaptured within 10 km of their original release location up to 14 years post-release (mean: 225 days), indicating some degree of site fidelity. However, 656 (14.2%) kingfish were recaptured over 100 km from their release location, with one fish travelling at least 2834 km in 702 days. Seasonal variability was evident for releases and

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recaptures, with more releases occurring in summer and autumn in most jurisdictions. Network analysis of recaptures revealed no connectivity between tagged kingfish from western and eastern Australia, supporting genetic delineation. By contrast, extensive connectivity exists across eastern Australia and NZ, with 87 kingfish moving between five Australian state jurisdictions, 316 individuals travelling across 15 bioregions and six kingfish moving between Australia and NZ. Our findings provide important new insights into the structure and connectivity of the eastern Australia kingfish stock and suggest increased collaboration between state and international fisheries jurisdictions may support improved stock assessment and management.

Keywords Fish tagging · Management · Movement · Network analysis · *Seriola lalandi* · Yellowtail kingfish

Introduction

Managing marine fish species for sustainability requires knowledge of life histories and ecology, particularly population dynamics (movement, connectivity), biological characteristics, and key habitat use (Fogarty & Botsford 2007). The generation of this knowledge is comparatively easier for species that undergo smaller movements, and use small spatial scales or less diverse habitats for the completion of their life histories. Conversely, highly

mobile pelagic fish species can travel 1,000s of kilometres and use a broad range of habitats across their life history (Altenritter et al. 2017; Baker et al. 2019; Rooker et al. 2007; Zeller et al. 1996). These species are often difficult to track due to the scale of their movements and their use of poorly observed offshore habitats (Hazen et al. 2012). Such habitats often encompass multiple fisheries jurisdictions (Begg et al. 1999; Huveneers et al. 2021; Lédée et al. 2021), presenting additional challenges to management (Pinsky et al. 2018). Differing exploitation rates, fishery regulations, and monitoring efforts among jurisdictional units can also confound individual assessments of stock health and sustainability.

Citizen-science programs have become particularly useful and instrumental in ecology, with increased stakeholder engagement allowing for cost-effective, wide-spread data collection (Brodie et al. 2018b; Hughes et al. 2022; Jaïne et al. 2012). These programs, managed and designed by scientists, can provide information over large spatio-temporal scales (Brodie et al. 2018b; Fowler et al. 2018; Hughes et al. 2022; Stewart et al. 2019). Mark-recapture methods have been used extensively to uncover many aspects of the life history of fish species. Genetic mark-recapture approaches can help estimate effective population size, structure and evolutionary connectivity (Andreotti et al. 2016; Bravington et al. 2016), while conventional investigations using physical tagging or marking can

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generate insights into species distributions, movements, growth, mortality, estimated population size and seasonal migrations (Brodie et al. 2018b; Couturier et al. 2014; Eveson et al. 2015; Henderson & Fabrizio 2014). The collection of tag-recapture data gained popularity in the mid-1900s as a means to understand fish movements, growth, survival and abundance (Jacobson et al. 2020; Paloheimo 1958; Schweigert & Schwarz 1993), and have been used to support the management of game fish species over the period since (Pepperell 2007). Although tag-recapture studies may yield low recapture rates (Gillanders et al. 2001), strong engagement and collaboration with recreational angler communities can yield higher recaptures or even, given appropriate training, higher tagging effort (Lucy & Davy 2000). Recreational angler tagging programs offer opportunities for scientists to gain broad-scale, long-term insights into the movement patterns of important fish species and help design more targeted studies for given species. Tag-recapture studies have many logistical challenges such as access to fishing facilities and remote areas, alongside associated costs such as the expertise required to capture the fish,

in addition to the temporal and geographical scales required to effectively answer ecologically relevant questions to the species. These citizen-science programs help overcome the logistical challenges and costs associated with operating over large-scale oceanic environments, lowering the costs of such research in the process (Begg et al. 1997; Morton et al. 1993).

Yellowtail kingfish (*Seriola lalandi*, Carangidae, hereafter ‘kingfish’) are a large, pelagic, predatory fish with a circumglobal distribution in temperate and subtropical waters (Gillanders et al. 2001; Nugroho et al. 2001; Poortenaar et al. 2001; Sepúlveda & González 2017). In Australia, mitochondrial DNA and microsatellite markers revealed two genetically distinct kingfish populations, or stocks (Green 2020; Miller et al. 2011); the Western Australian stock (restricted to the Australian west coast), and the Eastern Australian stock that encompasses the states of Queensland (QLD), New South Wales (NSW), Victoria (VIC), South Australia (SA), Tasmania (TAS), offshore seamounts and islands across the Tasman Sea (e.g. Lord Howe Island), and New Zealand (NZ) (Fig. 1). Within the Eastern Australian kingfish stock,

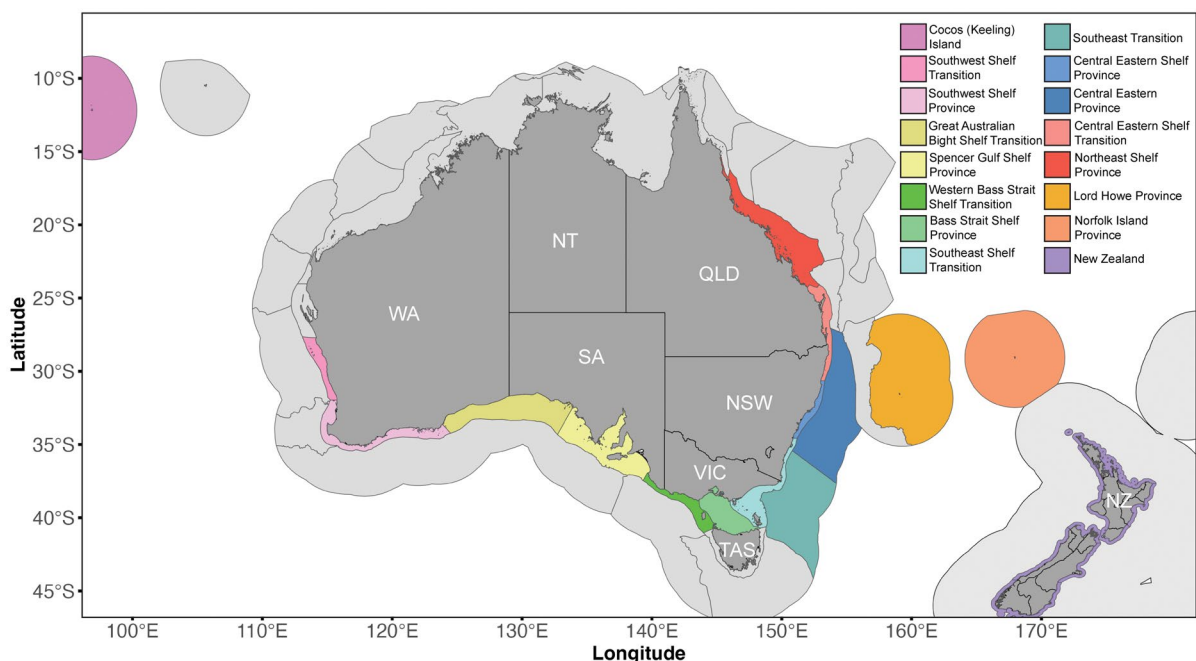


Fig. 1 Provincial bioregions (IMCRA, 2006) used to examine kingfish connectivity via network analysis of tag-recapture data from the New South Wales and New Zealand tagging programs. Grey shading represents bioregions with no tag-recapture records

evolutionary connectivity has been identified (Green 2020; Miller et al. 2011), but the extent of this connectivity between and within the various fisheries management jurisdictions in this region, and at a demographic rather than evolutionary level, is uncertain. Early tag-recapture studies in SA and NSW identified a degree of site affinity, with most tagged kingfish recaptured < 5 km from release locations in SA (Gillanders et al. 2001; Hutson et al. 2007), and < 50 km from release location in NSW (Gillanders et al. 2001). However, movements of up to 140 km and > 2000 km in the SA and NSW studies, respectively, were recorded. Recent acoustic tracking studies in NSW and SA also identified a similar degree of site affinity and individual variability in behaviour, with < 15% of tagged kingfish displaying broader-scale movements > 60 km from the release location (Brodie 2016). However, two kingfish acoustically tagged by Clarke et al. (2023) were observed to travel ~ 1800 km across four state jurisdictions in 191 days, highlighting the potential scale of movements across this region. The analyses reported in these studies, however, did not capture the full degree of mixing between the Western and Eastern Australian genetic stocks.

The range of the Eastern Australian kingfish stock encompasses two of the world's longest running recreational saltwater fish tagging programs, both established in the 1970s; the NSW Department of Primary Industries (DPI) Game Fish Tagging Program (NSW GFTP) (Pepperell 2007) and the NZ Gamefish Tagging Programme (NZ GFTP) (Saul & Holdsworth 1992). Kingfish are the second-most tagged species in both programs, with comparatively high recapture rates (NSW = 7.8%; NZ = 6.4%) (Holdsworth 2021; Pepperell et al. 2021). The high recapture rate of kingfish across both programs affords the opportunity to investigate long-term distribution patterns, movements, and connectivity of kingfish across an area of more than ~ 6 million km² spanning the entire range of the Eastern Australian biological stock. Recent stock assessments and workshops on kingfish in eastern Australia have identified a number of uncertainties and knowledge gaps, with further research on the distribution and movements of the spawning stock being a key research priority (Hughes et al. 2021; Hughes & Stewart 2020; Stewart et al. 2021).

In this study, we analysed half a century of tag and recapture records from the NSW GFTP and the NZ

GFTP to analyse kingfish movements, delineate the Eastern and Western Australia kingfish stocks, and quantify the degree of cross-jurisdictional connectivity across Australia and NZ waters, to better inform the appropriate spatial scale of management. We conducted several analyses on the tag-recapture data to ascertain the patterns in movement and connectivity across the entire Eastern and Western Australia kingfish stocks. First, we considered the tagging effort for kingfish versus all other species in the tag-recapture dataset. Second, we explored the seasonality of releases and recaptures, and assessed potential environmental and ontogenetic drivers on catch. Third, we assessed population connectivity using network analyses at broad- and fine- scales (bioregional and 1-degree grid, respectively). Finally, we examined patterns in individual behaviour to evaluate the variability within the population. By investigating multiple spatial and temporal scales of inference we aimed to provide a comprehensive trans-Tasman assessment of kingfish population structure and connectivity.

Materials and methods

Kingfish tag-recapture datasets

The NSW GFTP targets 60 species and over 500,000 tags have been deployed since 1973 by over 60,000 recreational anglers (Pepperell et al. 2021). The NZ GFTP is a cooperative effort between Fisheries NZ and the NZ Sport Fishing Council and anglers that began in 1975 and was initially focused on billfish species, but later expanded to other gamefish, including kingfish (Saul & Holdsworth 1992).

The NSW GFTP dataset consists of continuous tag and recaptures of kingfish between 1974 and 2022, while data from the NZ GFTP spanned 1978–2022. In both programs, suitable kingfish (i.e., > 70 cm total length (TL) in the NSW GFTP and > 65 cm fork length (FL) from 1978 to 2003, then > 75 cm FL from 2004—present in the NZ GFTP, in accordance with minimum legal length) were tagged with conventional pelagic streamer tags (Hallprint, Australia) inserted in the dorsal musculature and secured between the pterygiophores. Each released kingfish was assigned a unique ID, and the release location, date, length, and name of the angler releasing the fish were recorded. Length measurements provided by

anglers include a combination of fork and total length (in cm), although measurement type was not always reported. When missing, we assumed a measurement to reflect fork length, which avoided misclassifying immature kingfish as mature. When a kingfish was recaptured, its tag ID, recapture date, length, location, and angler name was recorded. Any records with the essential information missing were removed from the analyses.

To quantify possible biases in the dataset driven by tagging effort, records of all species released throughout the entire history of the program were obtained from the NSW GFTP. The release locations were averaged to the nearest degree of latitude and longitude to create a 1-degree network grid (as described in 3.3). The number of releases within each grid cell was then divided by the total number of releases to reveal the proportion of all releases that fell within that 1-degree cell. This was similarly conducted on the kingfish data so that the proportional kingfish tagging effort could be visually compared to total tagging effort for all other species. To further assess the potential impact of tagging effort on patterns observed in the dataset, a histogram of distance travelled was created for the recaptures of kingfish and non-kingfish species to identify potential trends in peaks of distances travelled by kingfish compared to overall effort in the tagging program.

Data cleaning and preparation

Kingfish release and recapture records were restricted to the combined Australian and NZ known range, with records $< 10^{\circ}\text{S}$ or beyond the Australian and NZ kingfish known longitudinal range removed (Hughes & Stewart 2020; Stuart-Smith et al. 2018). Across all records, 3079 releases did not include a date or accurate release locations and were removed from the analyses. Records that fell on land were removed, allowing for a 1 km buffer in the case of imprecise GPS coordinates (i.e., GPS rounding, locations inside estuaries or from land-based fishers). Records with biologically improbable length measurements for the species, i.e. > 190 cm FL (Stewart et al. 2001), and recapture dates earlier than release dates, were removed. Recaptures were filtered to only include fish that had an average speed between release and recapture location of < 7 km/hr, which was informed by diffusion rates used for track processing of pop-up

satellite archival tagged kingfish (Goddard, unpubl. data). Finally, we calculated the minimum distances travelled by each recaptured fish around land, taking into account the shape of the coastline as opposed to straight line distances crossing over land, using the RSP (Refined Shortest Paths) package in R (Niella et al. 2020).

All Australian kingfish tag-recaptures were allocated to Integrated Marine and Coastal Regionalisation of Australia (IMCRA) v4.0 Provincial Bioregions, hereafter referred to as ‘bioregions’, which are defined by the isobath, oceanographic habitat, and demersal fish assemblages (IMCRA, 2006). These bioregions range in size from 18,209 to 485,348 km², with potential movements across bioregions reflecting broad-scale movements across diverse habitats. Additionally, crossing of multiple bioregions generally resulted in traversing multiple fisheries jurisdictions, and therefore exposure to varying recreational and commercial management regulations. All coastal NZ releases and recaptures were allocated to a single bioregion for ease of interpretation of broad-scale trans-Tasman movements.

All analyses were performed using the statistical software R, version 4.2.1 (R Core Team 2021).

Seasonality of kingfish tagging

To assess potential variation in the seasonality of kingfish release and recaptures, density histograms were created for each jurisdiction (QLD, NSW, SA, VIC, Western Australia (WA), NZ), with release and recapture dates converted to Julian days, i.e. the corresponding numerical day of the year (e.g., January 1st = day 1). Temporal trends were explored visually for three size categories (at time of release), to evaluate the potential interaction between fish size and release/recapture patterns for each month of the year. These three size classes encompassed juveniles (< 50 cm FL), adults (> 83 cm FL), and an interim class of individuals undergoing maturation, that accounts for sex-specific differences in size at maturity (50–83 cm FL) (Gillanders et al. 1999).

Sea surface temperature (SST) for all kingfish catch records (i.e. releases and recaptures) was examined since it is a known driver of kingfish activity in the study region (Clarke et al. 2023). We extracted SST data at the time and location of release and recapture of all kingfish from the topmost layer in the

Bluelink ReANalysis (BRAN2020) global reanalysis (Chamberlain et al. 2021b). Sea surface temperature measurements were extracted using the *raster* package (Hijmans 2022) with a 10 km buffer around each of the reported locations to account for records that were in close proximity to land, or too shallow (i.e., estuaries). The BRAN2020 ocean model is data-assimilative with a 0.1° spatial cell resolution (Chamberlain et al. 2021a). Sea surface temperature from this model has been shown to be consistent with observations globally (Chamberlain et al. 2021b) and in the east Australian region (Schilling et al. 2022). Only kingfish catches occurring after 1993 ($n=49,450$) were considered for this seasonal analysis to match SST data availability.

Dispersal and connectivity

We plotted the relationships between time at liberty and the minimum distance travelled by tagged kingfish between their release and recapture locations to determine whether longer time at liberty promoted a larger minimum distance travelled. Trends in release jurisdiction and kingfish size were also examined, alongside temporal trends by grouping recaptures into yearly bins to further identify whether longer times at liberty promoted a larger minimum distance travelled.

To explore broad-scale movements and connectivity patterns of kingfish across the study region, a network analysis of the recapture data was performed. Each movement network consisted of nodes representing the bioregions of release or recapture, and edges denoting the number of observed movements between each pair of nodes. The resulting networks were constructed and visualised using the *igraph* R package (Csárdi & Nepusz 2006). We plotted the networks using two different visualisation layouts. A multidimensional scale layout helped examine the centrality patterns (i.e. which nodes or bioregions were more important for kingfish moving through the region), node density (i.e. the number of movements or edges existing between nodes or bioregions), and the bioregions that lacked high connectivity with others. In addition, a spatial layout provided insights into the spatial patterns of connectivity among all bioregions.

Five network level metrics were calculated to quantify the extent of overlap between each tagging program and connectivity patterns between

all nodes and edges in the overall network: (1) the number of incoming movements to a node, (2) the number of outgoing movements from a node, (3) the total number of unique movements between nodes (both incoming and outgoing), (4) the betweenness of each node (i.e. how likely a node is to be passed through when a kingfish moves from one node to every other node in the network), and (5) the closeness of the node to the other nodes in the network (i.e. how close a node is to others in the network based on shortest path distances of each movement to or from that node) (Table S1).

To identify finer-scale movements within and between state fisheries management jurisdictions, release and recapture locations were binned to the nearest degree of latitude and longitude to create a 1° network grid. Each 1° grid cell containing data was a node within the resulting network. Separate networks were created for the six fishery jurisdictions of kingfish releases (NSW, QLD, SA, VIC, WA and NZ) based on tag releases. The edges represented movements to other grid cells or nodes within the same jurisdiction, or outside the jurisdiction of release. The *igraph* R package (Csárdi & Nepusz 2006) was used to visualise the spatial connectivity of nodes within each of the six (state-based) networks.

Individual behavioural differences

We conducted a cluster analysis to assess variability in the behaviour of tagged Australian and NZ kingfish. Four input variables were used: release length, release month, minimum distance travelled, and time at liberty. Data were first normalised to remove any biases caused by outliers, specifically in the maximum distances travelled and time at liberty ($n=552$ recaptures removed). Hierarchical clusters were used to determine the appropriate number of clusters to inform *k*-means calculations (MacQueen 1967), with six clusters used for this analysis. A principal component analysis (PCA) was then conducted on the data using the *vegan* package in R (Oksanen et al. 2015). Principle component analyses were conducted on fish that were at liberty for at least 30 days ($n=2799$) before eventual recapture. We produced paired scatterplots for all input variable combinations to identify the key factors defining each cluster.

Results

A total of 63,432 kingfish were tagged and released across both programs and were assessed as part of this study. From April 1974 to February 2022, 39,755 kingfish were tagged and released by recreational anglers as part of the NSW GFTP, and 23,677 kingfish were tagged and released between May 1976 and June 2021 as part of the NZ GFTP. Kingfish had the highest recorded recapture rates of all teleost species in both the Australian (7.8%; $n = 3116$) and NZ (6.4% $n = 1525$) GFTPs, with tagging effort occurring throughout most of the species' range (Sup. Fig. 1).

Seasonality in kingfish tagging

Releases and recaptures of kingfish varied throughout the year and between fisheries management jurisdictions (Fig. 2). In all jurisdictions, most kingfish

were captured throughout the Austral spring–autumn months (September–May), with an observed decrease in kingfish captures in both programs during the winter months. In contrast, mature-sized kingfish (> 83 cm FL) in NSW appeared to be consistently available to the fishery throughout the year (Sup. Fig. 2), while highly seasonal in other jurisdictions, such as SA and NZ.

Overall, kingfish were released or recaptured across their range when SST ranged between 10.7 and 28.9°C (median 20.2°C and 20.7°C for Australia and NZ respectively, overall median = 20.3°C). Approximately half (50.8%, $n = 23,260$) of the releases and recaptures occurred when SST were between 18.7 and 21.5°C (1st to 3rd quartile range) (Sup. Fig. 3). However, SST upon release or recapture varied by state, with TAS recording the coolest median temperature (17.6°C) and QLD the highest (22.6°C) (Table S2). This was likely an artefact of the different

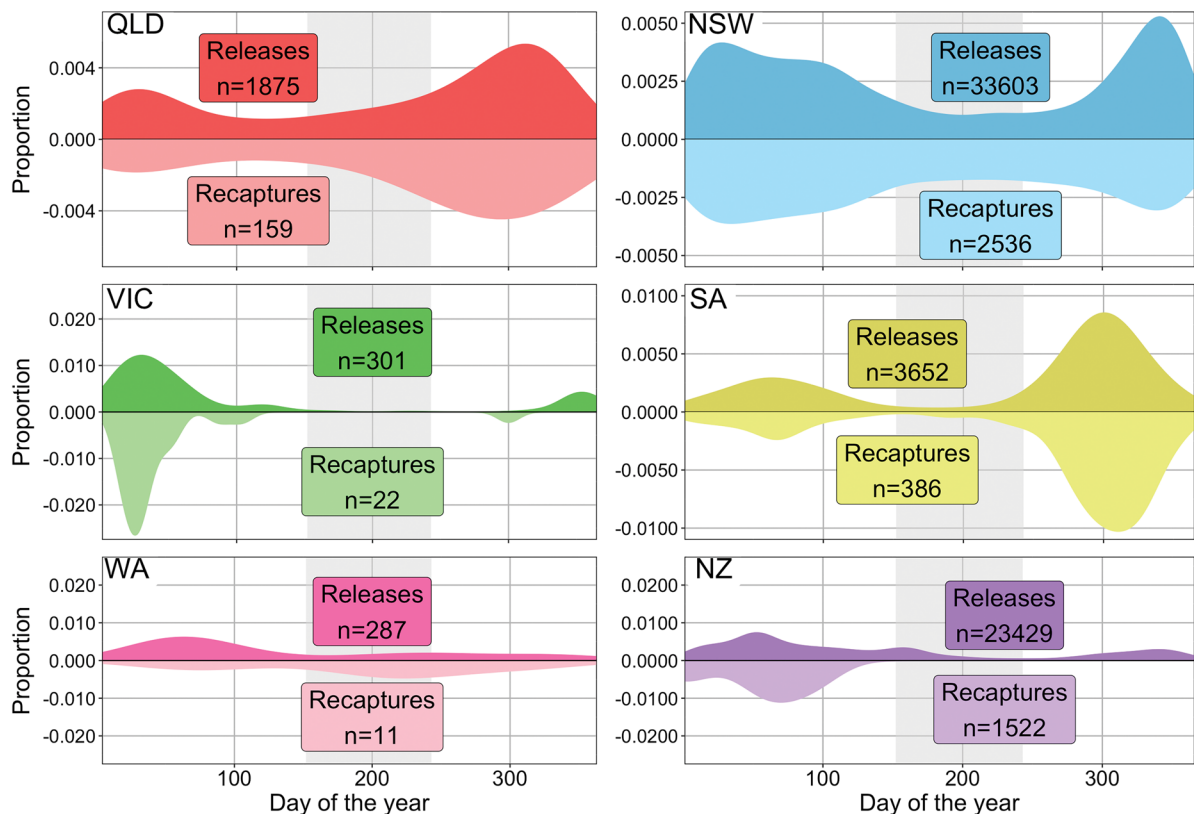


Fig. 2 Proportion of kingfish releases and recaptures throughout the year as part of the NSW and NZ game fish tagging programs. Releases in Tasmania and other jurisdictions are not

displayed because of the low number of records, or no recaptures. Light grey sectioning within each figure depicts the Austral winter months (June–August)

oceanographic and climatic habitats encompassed by those jurisdictions.

Dispersal

The 4636 kingfish recaptured over the study period showed variability in dispersal throughout Australian and NZ waters. Overall, tagged kingfish travelled a minimum distance of 0–2834 km (median \pm std dev: 9 ± 189.2 km) between release and recapture. Time at liberty also varied greatly,

with tagged fish being recaptured between 0 and 7222 days (47 ± 471 days) after release. Around half of the kingfish ($n = 1568$, 50.3%) tagged through the NSW GFTP were recaptured within two months of release (median \pm std dev: 60 ± 297 days; Fig. 3A), while kingfish from the NZ GFTP remained at liberty for longer (266 ± 871 days). In both programs, around half of tagged kingfish ($n = 2385$; 51.4%) were recaptured within 10 km of their release site (NSW GFTP: 11.4 ± 250.0 km; NZ GFTP: 7.8 ± 151.7 km).

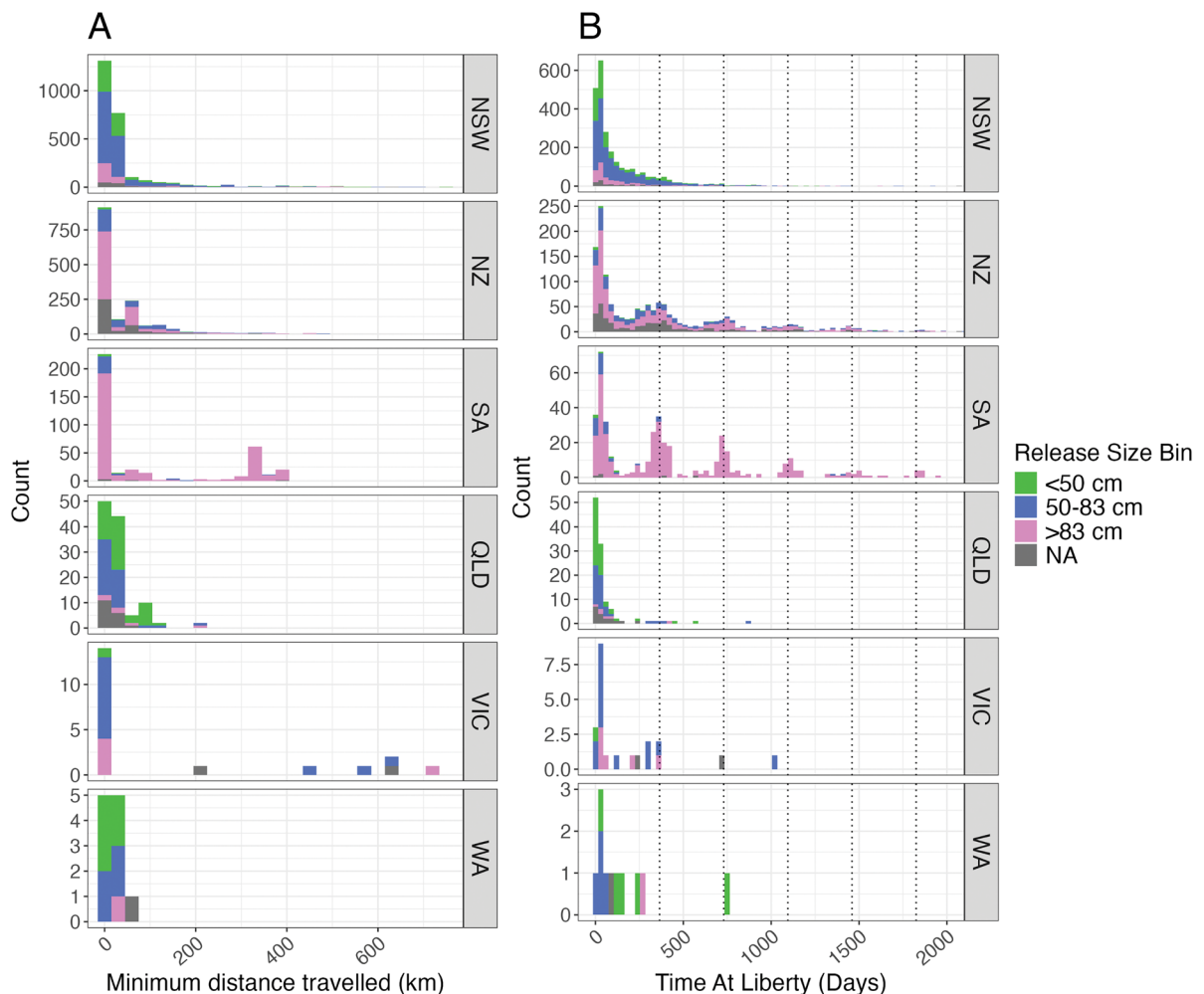


Fig. 3 Minimum distances travelled (i.e. distance between release and recapture) and time at liberty (i.e. days elapsed between release and recapture) for each tagged and recaptured kingfish in the NSW and NZ tagging programs. Minimum distance travelled (A) is limited to 750 km between release and recapture locations for ease of visualisation, with distances

grouped into 25 km bins. Time at liberty (B) is limited to 2,000 days for ease of visualisation, with dashed vertical lines every 365 days to highlight annual trends. Stacked histograms are coloured according to the size of the tagged kingfish at the time of release, with grey indicating fish where length was not recorded. Note the varying scales on the y-axes

Annual periodicity in kingfish recaptures was evident for SA and to a lesser extent for NZ (Fig. 3B). Notably, these two regions had the greatest proportion of adult kingfish tagged (> 83 cm). Kingfish in SA were generally recaptured at or near their release location, with a median distance between release and recapture of 0 km (1st quartile = 0 km; 3rd quartile = 322 km). Similarly, kingfish released in NZ were generally recaptured at or near their release location (median = 9.8 km; 1st quartile = 0 km; 3rd quartile = 61.2 km). By contrast, some kingfish ($n = 29$) released from SA also travelled considerable distances, being eventually recaptured in NSW or even QLD, with a maximum distance between release and recapture locations of 2,834 km in 702 days. There was a marked difference in movement behaviours between SA kingfish that displayed residency or high site fidelity (recaptured close to the site of release), and others that were more migratory (recaptured further away; Fig. 3). In other jurisdictions, kingfish recaptures exponentially decreased with time, with no evident relationship between time at liberty and minimum distance travelled (Fig. 3).

Connectivity

Network analysis revealed extensive connectivity of kingfish between 15 provincial bioregions across the study region (Fig. 4), indicating that kingfish can travel vast distances across varied habitats. The Southeast Shelf Transition and Central Eastern Shelf Province bioregions, encompassing shelf waters off most of NSW and northern VIC, recorded the highest centrality measures across nodes, and highest degree of connectivity to other nodes (bioregions) in the network (Table S1). Bidirectional movements were recorded between NZ and multiple bioregions across the Tasman Sea and off eastern Australia (Fig. 4). Despite observed connectivity across QLD, NSW, VIC, SA (hereafter referred to south-eastern Australia) and NZ, no connectivity was recorded between western and south-eastern Australia (Figs. 4 and 5). Offshore bioregions had the highest proportion of recaptures of tagged kingfish in a bioregion other than that of their release (Sup. Fig. 4). Over 88% of kingfish tagged in the Central Eastern Province and the Southeast Transition bioregions, offshore of NSW and northern VIC were recaptured in a different bioregion. The remaining bioregions recorded less than 15% of tagged kingfish recaptured in a different

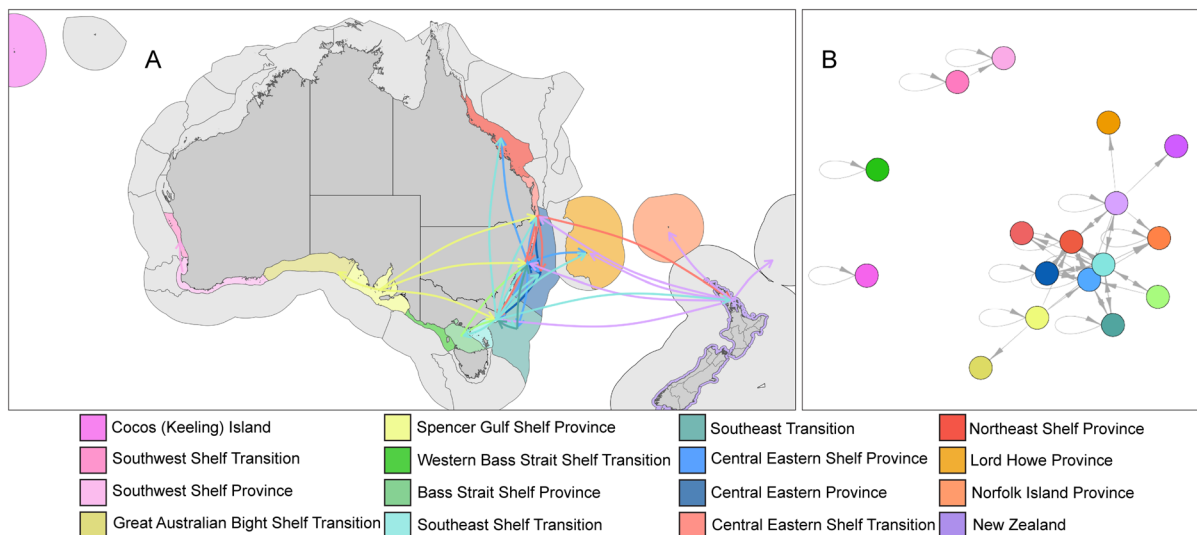


Fig. 4 Geospatial (a) and multidimensional (b) movement networks showing connectivity patterns of tagged kingfish between provincial bioregions. Australian kingfish releases and recaptures were allocated a corresponding bioregion according to the Integrated Marine and Coastal Regionalisation of Aus-

tralia v4.0—Provincial Bioregions (IMCRA, 2006) and New Zealand records were all grouped to the one point in the North Island for ease of visualisation (despite some releases occurring in the northern parts of the South Island)

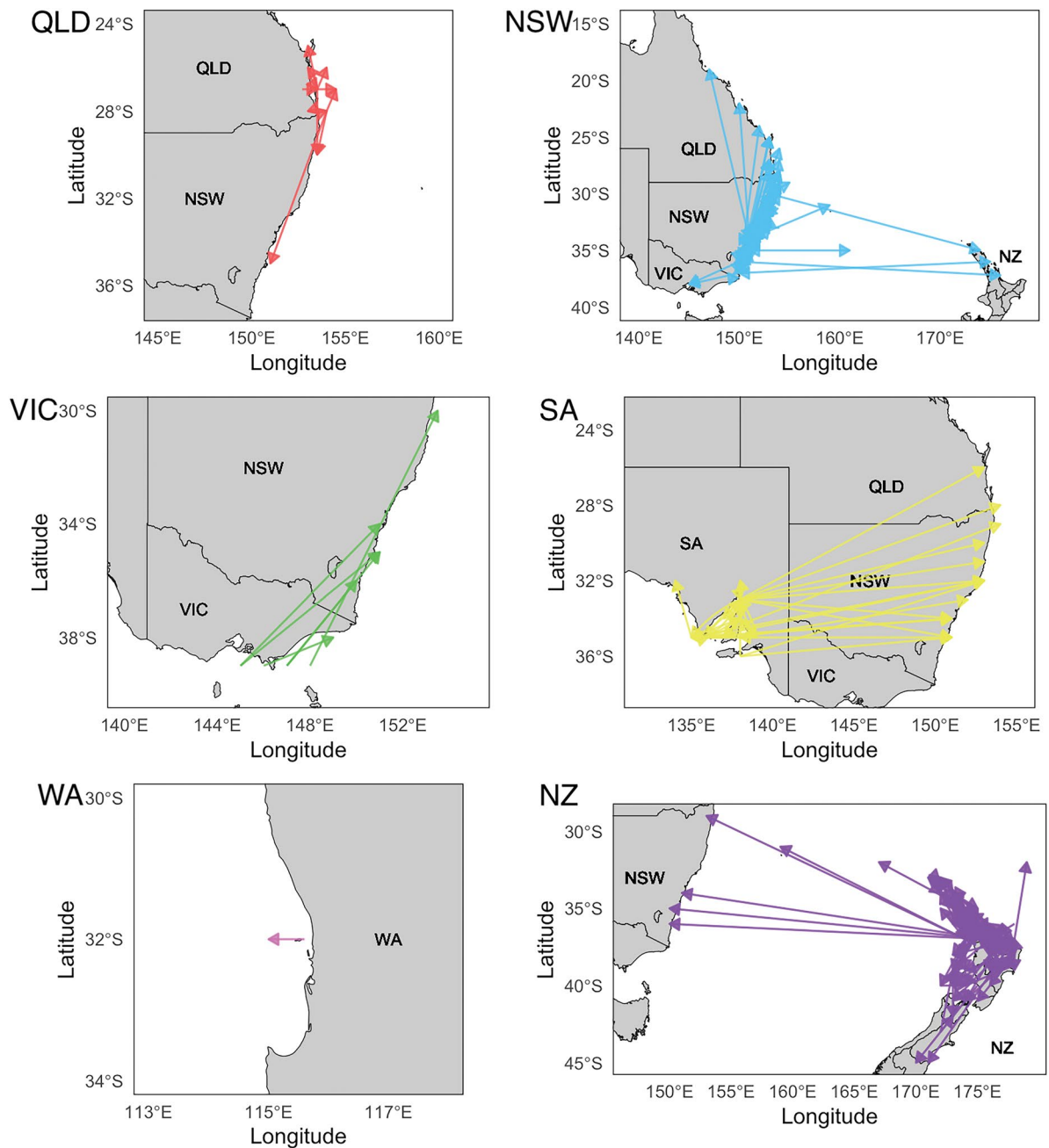


Fig. 5 Geospatial movement networks showing connectivity patterns of kingfish tagged and released in each fisheries management jurisdiction as part of the NSW and NZ tagging programs. Kingfish releases and recaptures are averaged to the

nearest whole latitude and longitude. Tasmania is not shown as no kingfish were recaptured within the state through either tagging program, despite having records of release

bioregion, except for the Bass Strait Shelf Province, where the two kingfish tagged in that bioregion were subsequently recaptured in a different bioregion.

Network analysis of kingfish recaptures across fisheries management jurisdictions showed clear delineation between kingfish tagged in WA and those

tagged in the other jurisdictions, with no observed movements between these regions (Fig. 5). In contrast, extensive connectivity was detected within and between south-eastern Australian jurisdictions and NZ (Fig. 5), with 87 cross-jurisdictional movements recorded. Most observed cross-jurisdictional movements originated from kingfish originally tagged and released in NSW and recaptured in QLD ($n=31$), followed closely by those released in SA and recaptured in NSW ($n=26$), and observed equal bidirectional movements between NSW and VIC ($n=7$ in each direction). No fish released outside of SA were recaptured in SA (Sup. Fig. 5). The observed cross-jurisdictional connectivity was minimally influenced by size class, with both juvenile and adults exhibiting movements between fisheries jurisdictions (Sup. Figs. 6 and 7).

Cluster analysis

Analysis of patterns in behaviour for tagged kingfish via PCA indicated that the relationship between kingfish recaptures was mostly similar, except for two clusters, defined by long times at liberty, or large minimum distances travelled (Fig. 6a). Release jurisdiction did not predict whether fish were more likely

to be at liberty for longer or travel a larger minimum distance (Fig. 6b). Release length also did not have a significant relationship with release month, time at liberty, or distance travelled.

Discussion

Our study is the first effort to combine nearly half a century of tag-recapture data from cooperative tagging programs across Australia and NZ to analyse movements and connectivity across the entire distributional range of the Eastern Australian kingfish biological stock. Our results support previous work on kingfish genetic stock structure in this region, with connectivity recorded among bioregions and jurisdictions within the Eastern Australian stock (Green 2020; Miller et al. 2011). Additionally, no kingfish tagged through the NSW or NZ GFTPs connected the Eastern and Western Australian stocks, supporting the genetic separation of the two (Miller et al. 2011). By contrast, the extensive trans-Tasman movements and cross-jurisdictional connectivity recorded between the south-eastern Australian states confirms that the Eastern Australian kingfish stock is likely to be a single stock throughout south-eastern Australia and

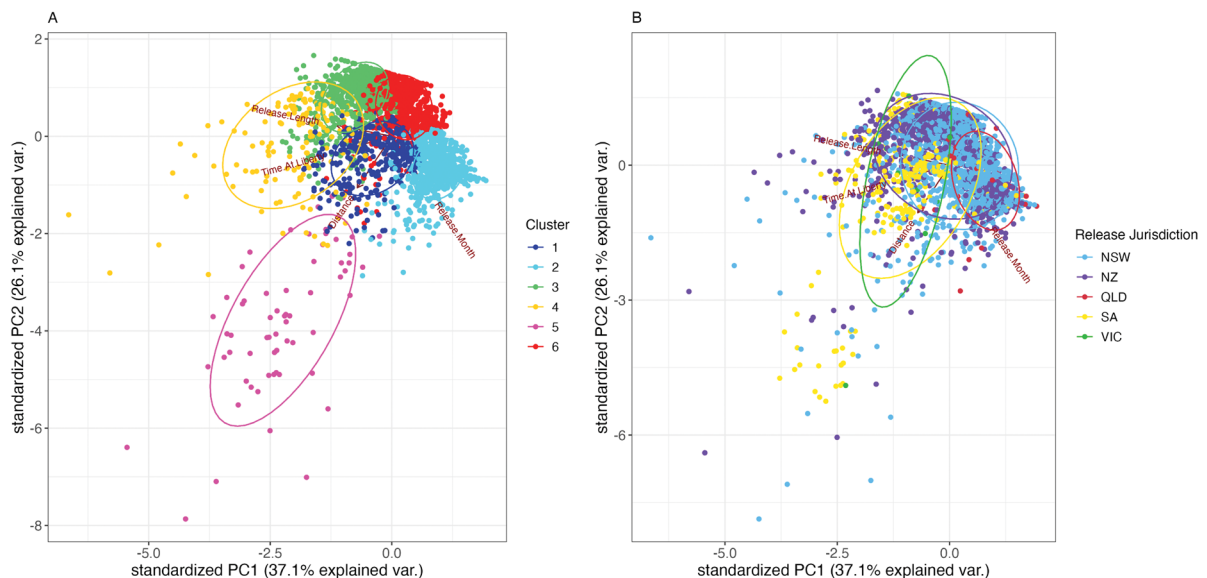


Fig. 6 Principal component analysis (PCA) of recaptured kingfish that were at liberty for at least 30 days. PCA (a) is coloured according to the cluster that kingfish were grouped into

based on having similar traits (i.e. time at liberty, minimum distance travelled, release length) and PCA (b) is coloured by the jurisdiction that each kingfish was released in

NZ. Cross-jurisdictional movements were observed across all life stages (i.e., juvenile, sub-adult, and mature-sized kingfish). Together, these findings suggest that assessment and management of kingfish across the Eastern Australian stock at the jurisdictional level may be enhanced by a multi-jurisdictional approach, with similar management objectives across jurisdictions.

Recreational and commercial kingfish fisheries are managed separately by each jurisdiction in Australia, with Australian and NZ fisheries also managed independently. The Eastern Australian kingfish stock was most recently classified as sustainable (Hughes & Stewart 2020), however this classification was largely based on data from the NSW component of the stock, with information from the other jurisdictions lacking. Legal minimum length for kingfish varies considerably between Australian states and NZ, from 45 cm TL in TAS to 75 cm FL in NZ (~85 cm TL), alongside bag limits which vary between one to five fish across the Australian states and NZ. Attitudes towards the tagging programs also vary by state and between individual anglers. The observed releases and recaptures of kingfish through both the NSW and NZ GFTPs are influenced by angler attitudes, with only a snapshot of the overall kingfish distributions and movements likely to have been captured in this study. For example, engagement in the program is far higher in NSW and SA than in VIC, which may have influenced the reported recaptures in this region. Where there was effort to tag kingfish across all size classes (i.e. NSW), it appears that the magnitude of kingfish dispersal movements, or affinity to the region of release, is independent of size (and age). The actual size of kingfish when broad-scale movements were initiated remains unknown, as kingfish may have been at liberty for many years, with the timing of broad-scale movements difficult to pinpoint from tag-recapture datasets.

Much of the information on kingfish connectivity among south-eastern Australian states has only been documented recently as a result of the increasing popularity of the NSW GFTP in SA, advances in electronic fish tagging technology (Hussey et al. 2015), and the ensuing development of Australia's continental acoustic telemetry network coordinated by the Integrated Marine Observing System's Animal Tracking Facility (Brodie et al. 2018a; Hoenner et al. 2018; Lédée et al. 2021). Additionally, the range extension

of this species associated with climate change has increased recreational fishing opportunities in TAS (Champion et al. 2018), and therefore led to increased tagging efforts in the region. Interestingly, the dataset analysed here and in Clarke et al. (2023), revealed unidirectional movements between SA and the eastern jurisdictions. However, very recent data from the NSW GFTP, occurring outside the main data collection period analysed here, includes the first recorded observation of a kingfish released in NSW (November 2021) being recaptured in SA (September 2023) (NSW DPI, unpubl. data). This recent recapture highlights the potential for more cross-jurisdictional movements and connectivity to be identified in the future through increased participation in recreational tagging programs and additional kingfish tagged with electronic transmitters.

The connectivity observed in this study, in conjunction with the minimum dispersal distances and time at liberty, suggest that kingfish exhibit a range of distinct movement patterns within the Eastern Australian stock. While most kingfish were recaptured close to their release site (51.4% recaptured within 10 km), there was also frequent cross-jurisdiction movements (14.5% recaptured over 100 km from release site). This is consistent with observations derived from acoustic telemetry in south-eastern Australia, where kingfish were typically site-attached with occasional broad-scale movements (Brodie et al. 2018a; Clarke et al. 2023). The concepts of metapopulation and partial migration are increasingly used to describe stocks where both residential and migratory individuals are present as 'contingents' within the overall population and display differing movement patterns (Chapman et al. 2012; Espinoza et al. 2016; Secor 1999; Setyawan et al. 2024; Thorold et al. 2001). The Eastern Australian kingfish stock may therefore provide yet another compelling example of a metapopulation with partial migration, encompassing both resident and migratory contingents within the stock. For example, kingfish captures in SA most commonly occurred during the Austral spring (October–November). Most of these fish were captured at the top of the Spencer Gulf, in Port Augusta, with anecdotal reports from anglers suggesting that these fish appear once SST exceeds 20°C. Some of the tagged kingfish were recaptured at this same site annually, suggesting a temporal affinity to the region. Despite being released at the same site,

other fish were recaptured in NSW and QLD (over 1,000 km distant). South Australia-released fish that were eventually recaptured in NSW or QLD ($n=29$) were recaptured during Austral spring–autumn, with the majority of fish recaptured in November ($n=9$) or October ($n=8$). Individual context, such as body condition, health, energetic state and genetic make-up have all been attributed as factors that may influence individual migratory behaviour (Lubitz et al. 2022) and may explain the variability in movement strategies observed here. Future research efforts using acoustic and satellite telemetry methods should also focus on defining environmental factors that influence kingfish movements and habitat usage.

Annual periodicity in recaptures was evident in both SA and NZ, where the release of kingfish was dominated by the adult size class. This annual signal in recaptures was not evident in any other jurisdiction where less adults were tagged. While the periodicity for NZ recaptures is likely driven by the increase in tagging effort during each February (coinciding with NZ Sport Fishing Council Nationals Tournament), questions remain for the SA recaptured kingfish. It is possible that this annual periodicity may have a biological driver, with sexually mature individuals returning to the same location to spawn. Conversely, this may be an artefact of the data, with the tagging effort in these jurisdictions being skewed towards adults, with the periodicity observed being biased by fisher behaviour in locations with typically cooler ocean temperatures. Further research is needed to ascertain the drivers of this apparent periodicity, as it could also be indicative of the formation of spawning aggregations for the species.

Despite the considerable insights generated by these extensive citizen science datasets, some aspects of the spatial ecology of kingfish remain unresolved. For example, kingfish released in SA have been recaptured in NSW and QLD waters but, to date, none have been recaptured in VIC or TAS waters, thus separating the two regions. This may be due to the broader, shallow shelf in the Bass Strait region that enables kingfish to transit further away from the coast, and therefore reduce their vulnerability to capture, given that most fishing efforts are concentrated in nearshore areas. Northern TAS has a lower human population density, with lesser tagging effort, reducing the likelihood of an angler encountering a tagged kingfish moving through the Bass Strait region. South

Australia-released kingfish that are recaptured in NSW and QLD may also be exhibiting “leapfrog” migration. This migration strategy has been described in birds and sharks, where animals from distributional limits bypass conspecifics in the centre of the species distribution (Lubitz et al. 2023; Ramos et al. 2015). This is driven by the timing of optimal breeding conditions, with offset breeding timing allowing for conspecifics to take advantage in surges of food availability in more distant locations (Bell 1996; Lubitz et al. 2022). The NSW GFTP has only recently expanded its tagging effort in other jurisdictions such as SA and VIC, and so more movements and cross-jurisdictional connectivity may therefore be captured in the future.

Kingfish have been observed to be available to Australian and NZ recreational anglers year-round, with releases and recaptures occurring throughout the entire year. However, both releases and recaptures of kingfish varied seasonally, with most occurring in the Austral spring–autumn months when SSTs ranged between 18 and 22°C. These SSTs encompass the thermal range for optimal kingfish growth and metabolic rate in aquaculture (Ilham & Fotedar 2016; Pirozzi & Booth 2009), but are marginally lower than the optimal temperatures predicted in kingfish distribution models which predict 22–22.5°C waters to be optimal habitats (Brodie et al. 2015; Champion et al. 2018). It is worth noting that the seasonal availability of kingfish is likely to have changed considerably since the commencement of the NSW and NZ GFTPs as the ocean off eastern Australia has warmed at over twice the global average rate in the past 50 years (Hobday & Pecl 2014; Malan et al. 2021). Southward distributional shifts have already increased availability to recreational and commercial fisheries in areas where the species has historically not been present (Champion et al. 2018). Verified citizen-science observations through the Range Extension Database and Mapping Project (Redmap; www.redmap.org.au) have recently recorded the occurrence of kingfish as far south as 43.5°S latitude off TAS (Stuart-Smith et al. 2018), extending their previously known range southwards by approximately 200 km. These observations are consistent with predictive models of kingfish distributions in the region, which suggest a poleward shift for this stock due to changing spatial habitat suitability (Champion et al. 2018, 2023). Additionally, fishing practices and equipment (i.e., sounders, gear-type, electric reels) have changed considerably

since the program's inception, which may have supported an expansion of fishing into additional regions. Together with the cross-jurisdictional connectivity observed in this study, shifting distributions of kingfish add a further layer of complexity for the management of this species.

Conclusions

Analysis of half a century of kingfish tag-recapture data collected by long-term citizen-science tagging programs provided highly valuable insights regarding the spatial ecology of the species across an area spanning ~6 million km² in Australian and NZ waters. Our results support the previous stock structure delineation between Western and Eastern Australia and reveal complex connectivity patterns within the Eastern Australian kingfish stock. Kingfish tagged as part of the Eastern Australian stock displayed both resident and broad-scale movement behaviours across multiple management jurisdictions and habitat bioregions. The movement patterns and cross-jurisdictional connectivity identified in this study confirm that the kingfish stock in this region is a single interconnected stock throughout south-eastern Australia and NZ. These cross-jurisdictional movements were observed across all size classes, suggesting that the spawning stock is shared among the entire range of the Eastern Australian biological stock. Together, our findings indicate that there may be advantages in moving towards multi-jurisdictional management strategies for the species. Further research should focus on examining environmental or biological triggers for kingfish migrations, specifically among mature individuals, and identifying key spawning areas, to further support management of the species. Finally, our multi-analysis approach presents a framework that is broadly applicable for analysing tag-recapture datasets derived from cooperative tagging programs to address questions about fish population structure, movement variability and cross-jurisdictional connectivity to inform fisheries management.

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Data availability The data used in this study are the property of the NSW Game Fish Tagging Program and the NZ Gamefish Tagging Programme. A copy of the dataset used in this study can be made available upon reasonable request and authorisation from the data owners.

Declarations

Conflict of interests The authors declare no conflict of interest with this research.

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