Original Research Paper – Fisheries Research

Movement patterns of an iconic recreational fish species, mulloway (*Argyrosomus japonicus*), revealed by cooperative citizen-science tagging programs in coastal eastern Australia.

Julian M. Hughes*[A], **Nicholas M. Meadows**[AB], **John Stewart**[A], **David J. Booth**[B] and **Ashley M. Fowler**[AB]

[A] New South Wales Department of Primary Industries, Sydney Institute of Marine Science. Building 19, Chowder Bay Road, Mosman, New South Wales 2088, Australia.

[B] School of Life Sciences, University of Technology, Sydney, NSW 2007, Australia.

*Corresponding author

Telephone: (+61 2) 9435 4671

Facsimile: (+61 2) 9969 8664

E-mail: Julian.Hughes@dpi.nsw.gov.au

Running head: Movement patterns of mulloway in eastern Australia

Additional keywords: Sciaenidae, connectivity, citizen science, population structure, spatial management

Author Contributions:
Julian M. Hughes – Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Supervision; Validation; Visualization; Writing - original draft; Writing - review & editing. **Nicholas M. Meadows** – Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Validation; Visualization, Writing - original draft. **John Stewart** – Conceptualization; Data curation; Investigation; Methodology; Supervision; Writing - original draft; Writing - review & editing. **David J. Booth –** Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Writing - review & editing. **Ashley M. Fowler** – Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Resources; Supervision; Software; Visualization; Writing - original draft; Writing - review & editing.

All co-authors have read and agreed to the current version of the manuscript.

Highlights

- ~~Knowledge of movement patterns are vital for management of exploited fish stocks.~~
- ~~Patterns of movement were therefore examined for *Argyrosomus japonicus* in eastern Australia.~~
- Released over 1000 km and three decades, tagged *Argyrosomus japonicus* were recaptured at a rate of 15.1%.
- Movements occurred predominantly over small spatial scales (<10 km) in eastern Australia.
- Fish tagged at lower latitudes, at larger sizes and over longer periods at liberty moved greater distances.
- Current spatial management of the stock may consequently need to be re-examined.
- Citizen science was key in the cost-effective generation of the broad-scale tagging dataset used.

Abstract

Information on the movements and population structure of an exploited fish species is vital for determining the appropriate spatial scale at which management should occur to ensure sustainable harvesting. However, such information exists for very few exploited recreational species. ~~Broad scale~~ Large-scale patterns and drivers of movement were ~~therefore~~ examined for an iconic recreational sciaenid species, mulloway (*Argyrosomus japonicus*), in coastal eastern Australia using an angler-assisted tag-recapture dataset. Over 4,300 individuals were tagged and released across 1,005 km of coastline over three decades (1988 – 2017). 657 individuals were subsequently recaptured at a rate of 15.1% over the same time period. Average time at liberty was 216 (± 9) days (range: 0 – 1,954 days) with distances moved ranging from 0 to 355 km. Median movement distance was 4 km and a large proportion of individuals (73%) were recaptured within 10 km of release locations. Thirty one percent of individuals were recaptured at release locations (<1 km) and 81% in the same estuary, however 7% moved distances of >100 km. ~~Linear regression also indicated that recapture latitude was strongly predicted by release latitude ($r^2 = 0.95$).~~ Generalised additive modelling revealed that release latitude, ~~season~~ body size and time at liberty were significant predictors of distance moved. Greater distances moved were observed for fish tagged at lower latitudes, ~~in autumn~~ at larger sizes and over longer periods at liberty. Results indicate that *A. japonicus* are primarily restricted to small movements (<10 km) in eastern Australia and display strong site fidelity, despite being capable of movements over larger scales (100s of km). This spatial scale of movement is also much smaller than the current 'jurisdictional' scale of management in this region (~1,000 km). Assessment and management of *A. japonicus* in eastern Australia may therefore need to be re-examined considering these findings and potentially undertaken at more localised spatial scales in the future. This study also highlights the importance of citizen science in the cost-effective generation of a sufficiently broad spatio-temporal dataset required to detect the movement patterns revealed here.

1. Introduction

Populations of organisms that occur over large spatial scales are frequently structured, consisting of multiple subpopulations that exist as discrete groups within the spatial extent of the overall population (Kritzer and Sale 2004). Information on the stock structure of an exploited fish species is vital for determining the appropriate spatial scale at which a species should be managed to ensure sustainable harvest (Begg et al. 1999, Pauly et al. 2002). The application of management measures that fail to recognise the extent of spatial stock structure can lead to localised depletions, and changes in demography, productivity and the genetic diversity of isolated stocks (Begg & Waldman 1999, Dominguez-Petit et al. 2008, Moore et al. 2011) without significant supplementation from neighbouring stocks (Bailey 1997). Despite the importance for management, spatial scales of population structure and connectivity remain unknown for most exploited marine fishes (Begg et al. 1999).

For spatially structured populations of marine species, connectivity is facilitated at two life history stages; by transport of eggs and larvae via oceanographic processes (Cowen & Sponaugle 2009), and by ~~direct migratory~~ movement of post-settlement stages (juveniles and adults) (Hughes et al. 2016). Both have the potential to significantly influence the genetic structure, demography and ecology of subpopulations (Cowen & Sponaugle 2009, Lowe & Allendorf 2010, Williams et al. 2012), which may have flow-on impacts on productivity and resilience to exploitation (Childs et al. 2015, Fowler et al. 2018). For most coastal ~~marine~~ species, the pelagic larval phase is the dominant dispersal stage with the potential for advection of scales of up to 1000s of km (Leis 2006). Consequently, considerable focus has been placed on this stage and the processes that influence it in addressing issues of population connectivity in marine systems (Cowen & Sponaugle 2009, Jones et al. 2009, Green et al. 2015).

However, direct ~~migratory~~ movements and dispersal of adults or juveniles has also been shown to take place over distances comparable to pelagic larval dispersal over seasonal and lifetime temporal scales (e.g. Hughes et al. 2016, Fowler et al. 2018, Brodie et al. 2018). Despite the ~~such critical~~ importance of such information, the influence of these movements on the stock structure of many exploited fish species are poorly understood (Begg et al. 1999, Gruss et al. 2011).~~Approaches used to examine the movements of post-settlement fish range from electronic radio, acoustic, satellite tagging (e.g. Taylor et al. 2006, Harasti et al. 2015, Lédée et al. 2021) to the use of natural tags like otolith elemental or isotopic composition (e.g. Ferguson et al. 2011, Hughes et al. 2016) and parasites (e.g. Poulin & Kamiya 2015). These techniques can deliver movement information at both fine individualised scales, as well as at the population scale, but are expensive, computationally-intensive, or both.~~ Mark-recapture techniques represent a traditional approach used to examine the movements of post-settlement fish,~~ Before the development and widespread use of such approaches, movement was traditionally investigated using mark-recapture techniques~~ providing individualised movement information based on the distance between release and recapture locations of tagged individuals (Hilborn et al. 1990). ~~Tag-recapture methods have the advantage of providing individualised movement information over large distances, with both a known start and finish location, but cannot resolve additional movement that potentially occurs between these two points during time at liberty (e.g. Takahashi et al. 2003).~~ Although tag-recapture studies provide little information on fine-scale behaviour of individuals, they are useful for investigating broad-scale patterns such as area utilization and the structure of movement by groups and populations of individuals (e.g. Takahashi et al. 2003, Espeland et al. 2008).

Tag-recapture investigations are in many cases subject to low recapture rates (Gillanders et al. 2001), but this shortcoming can be compensated for by the recruitment and participation of large numbers of recreational fishers to report recaptured individuals, or given appropriate training, conduct the tagging effort themselves (Lucy & Davy 2000). Cooperative recreational fisher tagging programs are a form of effective citizen science, where members of the public can voluntarily tag, release, and recapture certain fish species, thus contributing to robust data collection ~~using equipment and~~ within a framework designed and managed by professional scientists (e.g. Arlinghaus et al. 2007, Brodie et al. 2018). Although cooperative tag-recapture programs have a number of identified biases (e.g. Arnason & Mills 1981, Dunlop et al. 2013, Gil et al. 2017), they are~~ not only~~ able to provide movement information over extremely large spatiotemporal scales (e.g. Brodie et al. 2018, Fowler et al. 2018, Stewart et al. 2019)., ~~but are far more cost-effective and less~~

~~computationally-intensive than many of the abovementioned contemporary approaches.~~

Mulloway *Argyrosomus japonicus* (Temminck & Schlegel, 1844) is a large coastal sciaenid species widespread around southern Australia, the north-western Pacific Ocean and the Indian Ocean as far west as South Africa (Silberschneider & Gray 2008). It has a wide distribution in Australia, spanning more than 6,000 km from the Burnett River in Queensland, around the southern coast of the continent to North West Cape in Western Australia (WA; Silberschneider & Gray 2008). Within this broad distribution, *A. japonicus* occur around inshore rocky reefs and ocean beaches in nearshore coastal waters (<100 m depth) and are often abundant in estuaries and the lower reaches of rivers (Taylor et al. 2006, Silberschneider et al. 2009). Juveniles are found in estuarine and nearshore coastal environments, with estuaries representing a key nursery area (Gray & McDonall 1993, Silberschneider & Gray 2008). Significant commercial and recreational fisheries for the species are supported throughout these habitats with a long history of exploitation (Silberschneider & Gray 2008, Earl et al. 2018). The commercial catch of *A. japonicus* in Australia was reported to be in excess of 210 t in 2018, of which more than 70 t was taken from New South Wales (NSW) waters alone (Earl et al. 2018). The species is also a highly prized recreational target species with an estimated 260 t landed in 2013/14, again with a substantial proportion (103 t) taken in NSW waters (West et al. 2015, Earl et al. 2018). Heavy historical exploitation of the species has resulted in an 'overfished/depleted' assessment of the NSW component of the stock since 2004/05 (Silberschneider et al. 2009, Stewart et al. 2015, Earl et al. 2018) and has recently been subject to significant management changes in an effort to arrest the decline in *A. japonicus* fisheries here (Silberschneider et al. 2009, Earl et al. 2018).

In Australia, population genetic studies have revealed ~~regional differences in *A. japonicus* genetic analyses suggest~~ significant ~~broad~~ large-scale spatial structuring with the overall *A. japonicus* population divisible into four discrete genetic stocks - an east coast (NSW) stock, a west coast (WA) stock, and a stock in each of the eastern and western parts of the Great Australian Bight (Barnes et al. 2016). Current management of *A. japonicus* in Australian waters is undertaken at jurisdictional (state-wide) scales of 100s to 1000s of km, which roughly corresponds with this reported

~~broad~~ large-scale spatial stock structure (Earl et al. 2018). However, discriminant otolith morphology and chemistry analyses carried out in South Australia (SA) have shown evidence of much finer scale population sub-structuring within management units (Ferguson et al. 2011). In eastern Australia, spawning occurs in the lower reaches of estuaries and nearshore coastal waters between November and March (Silberschneider et al. 2009) with pelagic larvae recorded in offshore shelf waters (>30 km) between January and April (Neira et al. 1998, Smith 2003). This period corresponds with the highest seasonal intensity of the poleward flowing East Australian Current (EAC; Ridgway & Godfrey 1997) suggesting high potential for offshore mixing and considerable downstream advection of larvae driving consequent genetic homogeneity in this region.

Population structure and connectivity in the species may also be driven by the movement of post-settlement stages, however little is known about the ~~broad~~ large-scale movements of *A. japonicus* here (e.g. Taylor et al. 2006, Silberschneider & Gray 2008, Taylor et al. 2014). A synopsis of previous *A. japonicus* tagging studies in both Australia and South Africa indicate that juvenile fish (<2 years) appear to be relatively sedentary in estuaries, but sub-adults and adults can move greater distances (>200 km; Silberschneider & Gray 2008). Previous studies using small numbers of fish tagged with acoustic transmitters in estuaries have also shown that *A. japonicus* has a relatively small home range in both NSW (<17.7 km^2 in area; Taylor et al. 2006) and southern Africa (1.2 – 10.3 km in river length; Cowley et al. 2008, Næsje et al. 2012). Scales of connectivity and population structure may therefore exist over finer scales than that of current management of the biological (genetic) stock in this region.

To address knowledge gaps regarding large-scale and long-term movements, we aimed to ~~therefore~~ investigat~~ed~~ the movement patterns of *A. japonicus* in eastern Australia using an angler-assisted tag-recapture dataset covering 9.5° of latitude and spanning 30 years. Specific objectives included ~~ally, we aimed to~~: 1) determine the extent ~~and likelihood~~ of movement along the coast, 2) examine the levels of habitat connectivity and multiple estuary use, and 3) identify the influence of body size, time at liberty and latitude ~~and season~~ on movement distance ~~patterns biological and environmental factors influencing movement~~. This study provides ~~the first~~ key information on the ~~broad~~ large-scale movement patterns of *A. japonicus* in eastern

Australia, data essential for evaluating whether the current spatial scale of assessment and management are appropriate for the species in this region.

2. Materials & Methods

2.1 Tagging programs

Tagging of *A. japonicus* were undertaken by two NSW DPI Fisheries' initiatives, which were combined to create a large tag-recapture dataset. Between 1988 and 1994, *A. japonicus* were collected by research trawling in estuaries between the Richmond River and Burrill Lake spanning latitudes 28 to 35°S (Fig. 1; summarised in Silberschneider & Gray 2005, 2008). Most releases occurred on 29 occasions (May 1988 – November 1989) in the Richmond River, on 30 occasions (March 1988 – January 1990) in the Clarence River and on 37 occasions (November 1992 – November 1994) in the Shoalhaven River. Additional releases also occurred in Burrill Lake (once), Lake Conjola (12 occasions) and the Macleay River (3 occasions) between October 1990 and December 1994 (West 1993). Between 2013 and 2017, recreational anglers involved in a DPI Fisheries' citizen science initiative, the NSW Research Angler Program (dpi.nsw.gov.au/fishing/recreational/resources/fish-tagging/researchangler), captured and tagged *A. japonicus* from estuarine and nearshore marine waters from latitudes between 29 and 36°S (Fig. 1). Captured *A. japonicus* in both initiatives were measured to the nearest 0.1 cm total length (TL), tagged with a uniquely-numbered plastic single barb dart tag, and released. Fish captured by trawling were tagged with a 5 cm PDX tag and fish captured by angling were tagged with an 8 cm PDS tag (Hallprint Pty Ltd, South Australia). Information was also recorded on capture date and location. This information was also recorded when a tagged individual was recaptured by a recreational angler, commercial fisher or researcher. Individuals recaptured by recreational anglers were reported to the DPI Fisheries Gamefish Tagging Program (dpi.nsw.gov.au/fishing/recreational/resources/fish-tagging/game-fish-tagging).

2.2 Data processing

Data was checked for potential reporting errors prior to analysis. The coordinates of reported release and recapture location were checked in Google Earth

(earth.google.com/web/) and matched to location descriptions. Implausible or mismatched location coordinates were rectified where possible. Improbable fish lengths were defined using published size information for the species (Hutchins & Swainston 1986, Kuiter 1993) and removed. Linear distance between release and recapture locations was used to estimate distances moved (km) for each individual. Locations were recorded to 3 decimal degrees allowing for resolutions of approximately 0.093 km in an east-west direction and 0.107 km in a north-south direction. Individuals recorded moving less than these distances were therefore recorded as having a movement of 0 km.

2.3 Data analysis

Argyrosomus japonicus that were deemed to have moved a detectable distance were further investigated using a generalised additive model (GAM). The model was used to examine whether distance moved (km, hereafter “Distance”) was influenced by latitude of release (in degrees, hereafter “Latitude”), body size at release (total length in cm, hereafter “Length”) or days at liberty (hereafter “Days”)~~ or austral season of release (Spring, Summer, Autumn, Winter, hereafter “Season”)~~. GAMs were used following preliminary data exploration which indicated potentially complex non-linear relationships between the response variable and the continuous predictor variables. The gamma distribution with a log link was used due to the positive, continuous response variable and pattern of model residuals relative to that from an equivalent model employing the normal distribution. Model improvement using the gamma distribution relative to the normal distribution was confirmed through comparison of AIC values.

Modelling was conducted using the *gam* function in the ‘mgcv’ package (Wood 2011) in R (R Core Team Development Team). Smooth model terms were included for all continuous predictor variables~~, while “Season” was included as a parametric predictor~~. Selection of model terms and optimisation of smoothing functions was achieved automatically using the ‘select’ argument (with maximum likelihood estimation) within the *gam* function in the ‘mgcv’ package. This argument adds an extra penalty to each smooth so that terms with parameters that tend toward infinity are penalised to zero and dropped from the model (Marra & Wood 2011). The upper limit to the effective degrees of freedom (edf) for smooth terms was set at $k = 6$ to reduce model overfitting and the suitability of this choice was examined using the *gam.check* function to ensure edfs were not overly restricted. The deviance explained by the final model was used to assess the quality of the model fit.

Data were explored prior to analyses using boxplots, Cleveland plots and scatterplots following the protocol of Zuur et al. (2010). Potential concurvity among model terms was investigated using the *concurvity* function in the ‘mgcv’ package. Concurvity is a generalisation of co-linearity that occurs when a smooth term in a model could be approximated by one or more of the other smooth terms (Wood 2011).

3. Results

3.1 Tagging location and period

Overall, between 1988 and 2017, 4,357 *A. japonicus* individuals were tagged and released along 1,005 km of coastline between latitudes 28 to 36°S (Fig. 1). Releases were unevenly distributed along the coast, with 89% of individuals released in either latitudes 28-29°S (41.2%) or latitudes 33-34°S (48.2%), corresponding with the Northern Rivers and Greater Sydney – Shoalhaven regions, respectively. Releases were also unevenly distributed through time, with ~79% of individuals released in either 1988-89 (37.5%) or 2014-16 (41.8%).

Between 1988 and 1994, 2,510 *A. japonicus* of 16.5 – 72.6 cm TL (mean 32.6 ± 0.2 cm SE) caught by research trawling were tagged and released between latitudes 28 and 35°S, primarily in three major estuaries, the Richmond (46%), Clarence (21%) and Shoalhaven Rivers (31%; Fig. 1). The number of fish released per tagging event ranged between 1 and 157 with an average of 22.4 ± 3.0 (SE) fish released per event. The sizes of these fish revealed that the majority were likely juveniles. Between 2013 and 2017, 1,847 tagged fish of 35.0 – 155.5 cm TL (mean 74.0 ± 0.3 cm SE) were released by anglers in estuarine and nearshore marine waters between 28 and 36°S, with most (71%) occurring in the vicinity of Greater Sydney (Fig. 1). The vast majority (93.2%) of tagged fish were released in estuaries with only 6.8% of tagged fish released in nearshore marine waters. Fish tagged in estuaries ranged between 16.5

and 155.5 cm TL (mean 48.7 ± 0.4 cm SE) and fish tagged in nearshore marine waters ranged between 35.0 and 152.5 cm TL (mean 72.8 ± 1.2 cm SE).

3.2 Recapture location and period

Six hundred and fifty seven of the 4,357 tagged *A. japonicus* were subsequently recaptured at a recapture rate 15.1% (Fig. 1). The recapture rate of fish tagged by researchers and recreational fishers was 20.3% and 7.9%, respectively. Recaptures occurred over a period of 30 years from 1988 to 2017. Average time at liberty (± SE) was 215.7 (± 8.9) days (median 158 days) and ranged from 0 to 1954 days (~5.4 years). The time-at-liberty distribution was best described by a negative exponential function (y=12.849$^{-0.002x}$, where x is time-at-liberty). Length at recapture ranged from 26.0 to 147.0 cm TL. There were 18 fish that were recaptured more than once (17 fish recaptured twice, and one fish recaptured three times). For 15 of these, both recaptures occurred in the same location where the fish were originally tagged. For the other three fish, none were subsequently recaptured in the tagging location after being recaptured elsewhere.

Recaptures were recorded from 1,002 km of coastline between latitudes 26 and 35°S (Fig. 1). Latitudes with the greatest number of recaptures aligned closely with release latitudes, with 86% of individuals recaptured in the main release locations – either latitudes 33-34°S (56.3%) or latitudes 28-29°S (29.5%; Fig. 1). The most significant locations for recaptures were the Shoalhaven, Richmond, Clarence and Hawkesbury Rivers. Even though releases and recaptures occurred over a similar geographic range (~1000 km), some recaptures (2.6%) occurred at latitudes (26-27°S) further north than the most northern release latitude (28°S; Fig. 1). There were no recaptures recorded from 36°S, despite a small number of releases occurring at this latitude.

The vast majority (91.2%) of tagged fish were recaptured in estuaries with only 8.8% of recaptures occurring in nearshore marine waters. Most (86.0%) recaptured fish were both tagged and recaptured in estuaries, with just 1.2% tagged and recaptured in nearshore marine waters. 9.9% of recaptured fish were tagged in estuaries but recaptured in nearshore marine waters, and just 1.2% were tagged in nearshore marine waters and recaptured in an estuary. 80.5% of fish were tagged and recaptured in the same estuary with just 7.2% tagged and recaptured in different estuaries. For fish tagged in estuaries in the northern half of NSW (from Newcastle north; Fig. 1), 64.1% were recaptured in the same estuary and 15.0% were recaptured in a different estuary. In comparison, for fish tagged in estuaries in the southern half of NSW (from Newcastle south), a much higher proportion were recaptured in the same estuary (90.9%) with just 5.5% recaptured in a different estuary.

Median distance between tagging and recapture locations was 4.0 km, increasing to just 4.3 km when individuals at liberty for <30 days were excluded (Fig. 2). A large majority (72.6%) of tagged fish were captured within 10 km of their release location, 82.9% within 20 km and 89.0% within 50 km (Fig. 2). ~~Recapture latitude was strongly predicted by release latitude (linear regression; $r^2 = 0.95$, df = 656, $p < 0.001$; Fig. 3A) and this did not change when individuals at liberty <30 days were excluded ($r^2 = 0.95$, df = 580, $p < 0.001$; Fig. 3B).~~ A large proportion of fish (30.5%, 201 individuals) were recaptured at, or in close proximity (<1 km) to, their release location, spending between 0 and 934 days at liberty (~2.6 years). This proportion reduced to 28.3% when individuals at liberty <14 days were excluded and 25.5% when individuals at liberty <30 days were excluded. For fish originally caught by trawling ($n = 510$), distances between tag and recapture locations ranged from 0 to 355 km with an average (± SE) of 21.9 ± 2.3 km. Distances between tag and recapture locations for fish originally caught by angling ($n = 147$) ranged between 0 and 264 km with an average (± SE) of 15.6 ± 3.0 km. For fish initially caught in estuaries ($n = 630$), distances between tag and recapture locations ranged from 0 to 355 km with an average (± SE) of 20.2 ± 2.0 km. Distances between tagging and recapture locations for fish initially caught by in nearshore marine waters ($n = 27$) ranged between 0 and 264 km with an average (± SE) of 28.3 ± 11.7 km. The average time-at-liberty was 192.3 ± 7.7 days (range: 0 – 1,903 days, $n = 572$) for fish tagged and recaptured in estuaries and 285.4 ± 55.6 days (range: 15 – 838 days, $n = 18$) for fish tagged and recaptured in coastal waters.

A small proportion of fish (6.5%, 43 individuals) were recorded moving distances >100 km and were recaptured after an average of 187 days at liberty (Fig. 2). This reduced to 4.0% (26 individuals) for fish which moved >150 km and 2.3% (15 individuals) for fish moving >200 km with average time at liberty of 222 and 259 days, respectively. The largest movement recorded was 355 km and coincided with the longest period at liberty of 1,954 days (~5.4 years) for an individual tagged in the Richmond River (28.9ºS) when 27.4 cm TL and recaptured at Old Bar (32.0ºS) when 75.0 cm TL (Fig. 1). For the small proportion of fish (16.7% of the total, 110 individuals) which were recaptured north or south from their tagging locations, overall 60.9% (67 individuals) moved north and 39.1% (43 individuals) moved south (Fig. 3). For fish that moved north, distances ranged from 5 to 264 km with a mean (± SE) of 99.0 ± 7.8 km, and for fish that moved south, distances ranged from 4 to 355 km with a mean (± SE) of 99.3 ± 16.6 km. For fish tagged in the northern half of NSW (from Newcastle north; Fig. 1; *n*=81), movements occurred both north and south from release locations (Fig. 3A). However, for fish tagged in the southern half of NSW (from Newcastle south; *n*=29), movement direction was predominantly northwards from release locations (Fig. 3B).

3.3 Movement modelling

Model selection using the ‘select’ argument retained all predictor variables for distance moved (Fig. 4, Table 1). Latitude was a significant predictor of distance, with greater movement predicted for fish tagged at lower latitudes (Fig. 4A). Movement also increased rapidly with days at liberty until ~200 days, beyond which movement increased more gradually until a plateau was reached at ~700 days (Fig. 4B). An ~~marginal~~ increase in movement with body length was apparent between ~45 and 70 cm TL with only a marginal increase apparent beyond this length ~~which ~50 cm TL~~ (Fig. 4C)~~, but this effect was not significant at the α = 0.05 level (Table 1) with the largest 100 individuals (15%) showing the same median distance between tagging and recapture locations (4 km) as all recaptures combined (see 3.2)~~. ~~Less movement was predicted in summer relative to autumn, with intermediate values observed in spring and winter (Fig. 4D, Table 1).~~ Overall, the selected model explained only 35.8~~6.7~~% of null deviance.

4. Discussion

Despite being a species of considerable recreational and commercial value in eastern Australia, *A. japonicus* has been managed at the jurisdictional level (Earl et al. 2018), equivalent to ~9 degrees of latitude and >1000 km, without detailed knowledge of small-scale population structure and connectivity derived from direct examination of movement patterns. Instead, the current spatial scale of assessment and management corresponds with previous proposed *A. japonicus* population structuring which indicated an “East Coast” stock based on genetic analyses (Barnes et al. 2016). Our results indicate that, although some individuals can travel large distances (up to 355 km), the movement of the majority of *A. japonicus* are restricted to much smaller spatial scales than the current scale of management in eastern Australia. This is reflected by a median distance between tag and recapture locations of just 4 km, 73% of tagged individuals being captured <10 km from their release location and a high proportion of recaptures occurring at release locations (30%) or in the same estuary (81%), despite an average of >200 days between tagging and recapture.

The generally small scale of movement and strong estuarine site fidelity for *A. japonicus* in eastern Australia found in the current study is consistent with results of tag-recapture studies done on the species from South Africa (Griffiths 1996), which showed *A. japonicus* to be primarily resident with evidence of site fidelity and likely to be recaptured within 10 km of release locations or within the same estuary despite long periods at liberty (up to 1,713 days). Similar to results presented here, Griffiths (1996) also reported that only 5% of tagged fish moved >30 km, 3% >150 km and the greatest distance recorded was just ~250 km. Our results are also consistent with acoustic telemetry studies carried on the species in both eastern Australia (Taylor et al. 2006, 2014) and South Africa (Cowley et al. 2008, Næsje et al. 2012). For example, in the Georges River, eastern Australia, 21 acoustically-tagged *A. japonicus* were found to have a relatively small home range within the estuary (<17.7 km^2) and displayed strong site fidelity, with all individuals remaining within the estuary over a monitoring period of 11 months (Taylor et al. 2006). Similarly, in the Great Fish River estuary in South Africa, small numbers of juvenile *A. japonicus* implanted with acoustic transmitters moved distances within the estuary of 1.2 – 10.3 km over a period of ~6 months (Cowley et al. 2008, Næsje et al. 2012).

Despite the generally small scale of movement and strong estuarine site fidelity found in the present study, approximately 11% of individuals tagged in either estuarine or nearshore marine waters were subsequently recaptured in adjacent marine or estuarine habitats revealing the importance of habitat connectivity for the species in eastern Australia. Studies on the species in South Africa also showed that up to 60% of individuals tagged in estuaries undertook movements into adjacent nearshore marine waters where they remained for an average duration of ~3.5 days before returning (Cowley et al. 2008, Næsje et al. 2012). Similarly, Childs et al. (2015) showed that *A. japonicus* demonstrated high residency and site fidelity to tagging locations in both estuarine and marine waters, even though one third of tagged individuals visited adjacent marine or estuarine habitats.

Even though there was the potential for substantial increases in body size between release and recapture, a significant increase in distance moved was found with increasing size at release. Consistent with this finding, increased movement distances with increasing body size have been observed for many fish species from diverse families (e.g. Nottestad et al. 1999, Griffiths & Wilke 2002, Edgar et al. 2004) including sciaenids (e.g. Bacheler et al. 2009, Zarada et al. 2019). This pattern conforms to the models that body size drives maximum dispersal distance among species through its effects on metabolism and the cost of locomotion (Hein et al. 2012). For example, there was a significant relationship between fish length and movement distance found for *Sciaenops ocellatus*~~the temperate reef labrid *Notolabrus tetricus*~~, which were shown to ~~display reduced site fidelity and~~ be at large for longer and travel significantly larger distances with increased body size (Bacheler et al. 2009~~Edgar et al. 2004~~). Similarly, Zarada et al. (2019) were able to show that maximum distance travelled was greater for larger female *Cynoscion nebulosus* than for smaller males over three seasons at a spawning aggregation site. ~~had a the extent of migration increases with increasing body length for a suite of pelagic planktivores (*Clupea harengus, Micromestistius poutassou, Scomber scombrus* and *Mallotus villosus*).~~ For *A. japonicus*, Taylor et al. (2006) showed that home ranges and daily movements within an individual estuary were significantly correlated with body length – large individuals moved further and had a larger home range than smaller individuals. Even though residence in each habitat in the present study was similar, a larger proportion (~10%) of fish recaptured in coastal waters had been tagged in an estuary compared with just ~1% of fish recaptured in an estuary after being tagged in coastal waters. In combination with the overall larger size of individuals both tagged and recaptured in marine waters (73 cm *cf* 49 cm TL), this suggests the potential for a general life-history driven movement from estuaries to the open coast with increasing size. Childs et al. (2015) also showed that the number of marine excursions undertaken by juvenile *A. japonicus* tagged in estuaries was positively related to fish length.

Many such relationships between fish size and movement distance are also often related to size-at-maturity (e.g. Griffiths & Wilke 2002, Maggs et al. 2019). For example, adult *S. ocellatus* were shown to move progressively larger distances than juveniles related to movements from estuaries into spawning habitat in offshore waters (Bacheler et al. 2009). Similarly, Maggs et al. (2019) showed that life history stage was a significant predictor of wide-ranging movement behaviour in the teleosts *Lutjanus rivulatus*, *Lichia amia* and *Dichistius capensis* as well as two species of elasmobranchs. It has been previously suggested that as fish reach maturity, *A. japonicus* begin undertaking extended coastal long shore spawning migrations in both eastern Australia (~~~80 cm TL;~~ West 1993) and ~~southern~~ South Africa (~~~100 cm TL;~~ Griffiths 1996). Modelling results from the present study are ~~somewhat~~ consistent with this suggestion, which shows that for the small proportion of individuals which did move, there was a ~~slight, but non-~~significant increase in movement with body length beyond ~45 cm TL. While smaller than the size-at-maturity for female *A. japonicus* (68 cm TL), this length corresponds to the size-at-maturity for male *A. japonicus* (Silberschneider et al. 2009) and the size at which sensory and caudal fin development of *A. japonicus* begin to plateau in south eastern Australia (Taylor et al. 2020). Griffiths (1996) also showed that of the small proportion of *A. japonicus* that did move substantial distances in South Africa, distances moved by mature-sized individuals were slightly larger than those moved by immature-sized individuals. Evidence consistent with a spawning migration in the present study was also provided by the very similar distances moved in either north or south directions (~100 km) for the small proportion of individuals which were recaptured north or south of their tagging locations, potentially representing movements to and from spawning locations. The movement patterns exhibited by these fish are consistent with previous studies on *A. japonicus* from South Africa, where the species movement type has been described as ‘resident/migratory’ displaying primarily ‘station-keeping’ behaviour together with less common periodic ‘migratory’ behaviour (Griffiths 1996, Mann et al. 2015).

Alternatively, the large variation in distances moved by individuals may be related to different contingents within *A. japonicus* populations which exhibit different movement behaviour (*sensu* Secor 1999). A small number of *A. japonicus* individuals in the current study were demonstrated to have moved 100s of km over a sub-yearly temporal scale (e.g. two individuals moved ~300 km in 4-5 months), confirming the movement capabilities of the species (Barnes et al. 2019), however most (73%) were recaptured within 10 km of release locations (including 30% at the release location itself and 81% in the same estuary) after an average of >200 days at liberty. It therefore appears that although most *A. japonicus* are highly resident displaying strong site fidelity ~~or homing behaviour~~, others display less site fidelity and undertake extensive long-distance movements. Multiple contingents which exhibit variable movement behaviours have also been previously demonstrated to occur in numerous other species of fish from both marine (e.g. Boje 2002, Fukumori et al. 2008, ~~Harasti et al. 2015,~~ Conroy et al. 2018, Fowler et al. 2016, 2018) and freshwater environments (e.g. Jonsson & Jonsson 1993, Morinville & Rasmussen 2006, Comte & Olden 2018). Childs et al. (2015) have suggested that high levels of residency *A. japonicus* in South Africa may indicate that juveniles exist as metapopulations consisting primarily of non-dispersing subpopulations, each with distinct estuarine and marine contingents; connectivity between habitats driven by the small number of individuals that display exploratory/migratory behaviour (Secor 1999) and best described as ‘partial migration’ (Kerr et al. 2009).

The distances moved by *A. japonicus* in this study suggest high potential for demographic sub-structuring within the eastern Australian population. Just 7% of individuals were recaptured >100 km from their release location, suggesting that locations separated by greater distances may experience extremely limited exchange of individuals through post-settlement movement. Given the distributional range of *A. japonicus* in eastern Australia (>1000 km), exchange of individuals is therefore likely restricted between at least some parts of the coast. As with all tag-recapture studies, the direct distance between tagging and recapture locations is likely an underestimate of actual total distances moved by individuals (e.g. Takahashi et al. 2003, Attwood & Cowley 2005, Fowler et al. 2018, Stewart et al. 2019). Together with the lack of multiple estuary use found in the current study, there is also considerable evidence from finer-scale acoustic telemetry studies that *A. japonicus* likely exhibits strong site fidelity to natal estuaries and homing behaviour (Taylor et al. 2006, Cowley et al. 2008, Næsje et al. 2012, Childs et al. 2015). For example, both Cowley et al. (2008) and Næsje et al. (2012) showed that even though some individuals made repeated excursions to the ocean adjacent to the estuary of residence, all individuals returned to the estuary each time.

~~Long-shore spawning migrations in coastal waters have also been observed to occur in both Australia (West 1992) and southern Africa (Griffiths 1996), with individuals hypothesised to make a post-spawning return migration. Although our modelling found a significant effect Season on *A. japonicus* movement, despite a considerable proportion (0.14 – 0.29) of tagged fish being of mature sizes. In fact, summer was the season when the least movement was predicted, despite movements related to spawning likely occurring primarily during the summer spawning period for *A. japonicus* in eastern Australia (November-March; Silberschneider et al. 2009, Taylor et al. 2014). The limited and counter-intuitive effect of season on movement may be a result of the strong site fidelity and homing behaviour demonstrated for *A. japonicus* in this, and other studies on the species (Taylor et al. 2006, Cowley et al. 2008, Næsje et al. 2012, Childs et al. 2015), with movement primarily occurring over short distances between estuaries and adjacent coastal spawning areas. Such small movements would reduce the model's ability to detect temporal relationships, particularly given the coarse categorical nature of the Season factor used in the current study. Future investigations should consider resolving sub-annual temporal relationships to the level of month, if sufficient data is available at that level.~~

Limited exchange of individuals may lead to variation in demography among *A. japonicus* populations along eastern Australia driven by spatial variation in environmental conditions, historic and current fishing pressure, or a combination (e.g. Williams et al. 2003, D'Anatro et al. 2011, Hughes et al. 2017, Fowler et al. 2018). In eastern Australia, there exists a strong latitudinal environmental gradient from north to south in water temperature (Ridgway & Dunn 2003), nutrient loads (Rochford 1984) and productivity (Suthers et al. 2011), driven primarily by the activity of the dominant oceanographic feature in the region, the poleward flowing East Australian Current (EAC). For fish species with distributions which span similar latitudinal scales, this environmental gradient may influence the productivity and demographic characteristics of fish populations, such as growth, mortality and longevity at smaller spatial scales (e.g. Kuparinen et al. 2016, Hughes et al. 2017). There is also evidence of latitudinal variation in historical fishing pressure on *A. japonicus*, with populations in central NSW historically subject to greater fishing pressure than those further north (Silberschneider et al. 2009, NSW DPI unpublished data). This has resulted in historical declines in commercial landings of *A. japonicus* in central NSW from at least the 1980s onwards (Silberschneider et al. 2009, NSW DPI unpublished data). Such sustained fishing pressure may result in the truncation of size and age structures of populations due to the systematic removal of large, old individuals (Stewart 2011), which our movement patterns demonstrate would not be replaced substantially by immigration from neighbouring areas. Indeed, there is evidence of a temporal change in the length structure of *A. japonicus* in this region, with substantial reductions in the proportion of fish of mature lengths in commercial landings from the mid-1990s through to the mid-2000s (Silberschneider et al. 2009, NSW DPI unpublished data). The consequences of such limited exchange of individuals must therefore be considered together with the effects of fishing pressure and environmental change on the demographic structure of eastern Australian *A. japonicus* populations.

Whilst limited spatial exchange of individuals demonstrated by this study is likely to influence demographic sub-structuring of the *A. japonicus* population in this region, it is unlikely to influence the overall genetic structure of *A. japonicus* in eastern Australia. *Argyrosomus japonicus* possess pelagic eggs and larvae (Neira et al. 1998, Smith 2003) which are spawned in the lower reaches of estuaries and in nearshore marine waters around the mouths of estuaries and in surf zones between November and March (Silberschneider et al. 2009, Taylor et al. 2014). Dispersal of these life history stages routinely occurs over much larger spatial scales (100s – 1000s of km; Leis 2006) than the movements described here. In addition, downstream advection via the poleward flowing EAC would potentially be maximised during the spawning season for *A. japonicus* in eastern Australia, which is also when the strength and intensity of the EAC is at its greatest (Ridgway & Godfrey 1997). The homogenous genetic structure of *A. japonicus* in eastern Australia (Barnes et al. 2016) is therefore likely determined primarily by larval dispersal patterns rather than the movement of post-settlements life history stages as so few individuals move over comparable spatial scales. Management of the *A. japonicus* fishery in South Australia also assumes a single stock, based on genetics (Barnes et al. 2016), however regional differences in the elemental chemistry and morphology of otoliths suggest that three separate populations occur along eastern, central and western coasts of South Australia (Ferguson et al. 2011). The spatial separation of these populations in South Australia (~150 – 450 km) are considerably larger than the scales of movement routinely demonstrated here for *A. japonicus* in eastern Australia and were also shown to be consistent with regional differences in demographic characteristics (Ferguson et al. 2008, 2014). Griffiths & Hecht (1995) have similarly suggested that whilst the population of *A. japonicus* in South Africa is likely a single genetic stock, analysis of otolith shape and demographic parameters indicates at least three separate regional populations.

Latitude was found to be a significant predictor of movement for *A. japonicus* in the current study. Fish released at lower latitudes moved greater distances both north and south from release locations compared with those released at higher latitudes, which moved smaller distances and primarily north. A higher degree of multiple estuary use was also evident in the northern part of the study region revealed by the 15.0% of estuary releases that were recaptured in different estuaries in the north compared with just 5.5% in the southern part of the study region. The NSW coast contains 184 estuary systems; however, they are unevenly distributed over the 1090 km spatial extent of the state’s coastline with a much greater density in southern NSW than further north (West et al. 1985). There are almost twice as many estuaries in southern NSW (89) than there are in northern NSW (55) with concomitant distances between major estuary systems greater in northern NSW than further south. For example, there are just 12 estuaries in the ~150 km between the major estuary systems Tweed and Clarence Rivers in northern NSW (~28-29°S). In comparison, over a comparable distance between the Shoalhaven River and Wagonga Inlet systems in southern NSW (~35-36°S), there are 34 estuaries. Because of the demonstrated importance of estuaries for *A. japonicus* (Taylor et al. 2006, Cowley et al. 2008, Næsje et al. 2012, Taylor et al. 2014), the small number of individuals which do move are therefore likely to move between estuary systems. Combined with the overall small scale of movement and low degree of multiple estuary use in southern NSW, it is thus likely that any inter-estuarine movements are more likely to occur between estuaries that are in close proximity to one another, as occurs in southern NSW. The larger distances moved by *A. japonicus* in northern NSW are therefore potentially related to the higher degree of multiple estuary use, movement in both directions, and the increased distances between estuaries in the region north of ~30ºS.

This study contributes to a growing body of work which demonstrates the value that can be added to studies of movement of recreationally-important fish species by the involvement of anglers (e.g. Brodie et al. 2018, Fowler et al. 2018, Stewart et al. 2019). Primarily by utilising recreational anglers to report the capture of tagged individuals, this study was able to examine the movements of *A. japonicus* at large spatial and temporal scales (>1000 km over 30 years). Such scales would be difficult to achieve in a cost-effective manner using many contemporary approaches (e.g. radio, acoustic, or satellite tagging, otolith elemental or isotope composition, parasites). This large spatio-temporal scale is particularly valuable for examining the movements of species like *A. japonicus*, which this study has shown are capable of occasional long-distance movements (100s of km) that may occur over extended time periods (~5 years) because the chance of capturing such movements are greatly increased.

However, despite the demonstrated value of angler-assisted tag-recapture datasets, they do have several acknowledged biases and limitations (e.g. Arnason & Mills 1981, Gillanders et al. 2001, Dunlop et al. 2013, Gil et al. 2017). One such bias in the current dataset concerns the spatial variability in patterns of recreational fisher effort which may have influenced relative release and recapture patterns (Bacheler et al. 2009, Fowler et al. 2018). In this study, patterns of *A. japonicus* recaptures suggested that recreational fisher effort was likely higher in some key estuaries such as the Richmond (~28ºS), Clarence (~29ºS), Hawkesbury (~33ºS) and Shoalhaven Rivers (~34ºS), than elsewhere in eastern Australia. When combined with the strong site fidelity demonstrated for the species here, anecdotal evidence regarding the popularity of these estuaries with recreational *A. japonicus* fishers (West 1992), could have resulted in shorter distances being estimated between tagging and recapture, because individuals released in these specific estuaries were more likely to be recaptured there than at locations further away. Ultimately however, fine-scale recreational fishing surveys (e.g. Steffe et al. 2007) would be required to fully understand spatial and temporal patterns in effort for *A. japonicus* in this region at the spatial scale of individual estuaries to detect, and correct for, such a bias. Even when appropriately trained, using anglers to carry out the tagging effort in tag-recapture studies may also result in higher post-release mortality and tag loss than when carried out by trained scientists, due to a lack of experience and the consequent use of suboptimal handling and tagging procedures. *Argyrosomus japonicus* are also a species which are particularly susceptible to barotrauma which does affect their survival after tagging, even over long periods post-release (~~Hughes & Stewart 2013,~~ Hughes et al. 2019). In the current study, more than 40% of *A. japonicus* individuals were tagged by anglers, with the remainder tagged by researchers. This may have increased mortality of fish tagged offshore, reducing recapture rates from this environment. Although the above issues could not be specifically addressed in the current study, none of them would be expected to influence estimates of actual distances moved.

The fisheries for *A. japonicus* in NSW have been in decline since at least the mid-1970s and the ‘East Coast’ genetic stock has been assessed to be ‘depleted’ or ‘overfished’ since the early-2000s (Silberschneider et al. 2009). Despite substantial management changes implemented to arrest the decline in commercial and recreational fisheries for *A. japonicus* in NSW, the stock continues to remain in a ‘depleted’ state (Earl et al. 2018). This situation may partly relate to findings from our work which demonstrates that despite being capable of moving long distances, *A. japonicus* generally exhibits extremely restricted movement patterns and strong estuarine site fidelity in this region, a combination of features which have previously been suggested to result in increased vulnerability to exploitation for the species in South Africa (Childs et al. 2015). Such increased vulnerability is potentially manifested in the high (15.1%) recapture rate recorded for *A. japonicus* in this study, a rate more than double that of any other species tagged as part of the NSW Gamefish Tagging Program (NSW DPI 2020). In the presence of spatially variable historical fishing pressure and environmental gradients, such limited connectivity may have led to demographic population structuring at spatial scales (<10 km) which are potentially several orders of magnitude smaller than the current ‘jurisdictional’ scale of management (>1000 km) for the species in this region. A re-examination of the appropriateness of current spatial scales of assessment and management for *A. japonicus* in eastern Australia is therefore strongly recommended with future assessment and management potentially required at substantially smaller spatial scales (e.g. individual estuaries or catchments) in order to sustain local fisheries.

This conclusion is consistent with the increasing evidence that species from disparate fish families which exhibit limited movement can drive small-scale demographic population structuring, even if some individuals demonstrate movement abilities over much larger spatial scales (e.g. *Mugil cephalus*; Fowler et al. 2016, *Arripis trutta*; Hughes et al. 2016, *Sardinops sagax*; Izzo et al. 2017, *Pseudocaranx georgianus*; Fowler et al. 2018, *Chrysophrys auratus*; Stewart et al. 2019). An in-depth understanding of such population sub-structuring and patterns of connectivity are therefore integral to successful holistic fisheries management practices (Begg et al. 1999, Goethel et al. 2011, Ferguson et al. 2011). This study demonstrates how traditional tag-recapture studies can contribute to this understanding of the demography of species with broad distributions and high swimming abilities instead of more expensive and computationally-intensive approaches such as acoustic telemetry or otolith chemistry. This study also highlights the importance of citizen science in the cost-effective generation of a dataset with sufficiently large spatio-temporal coverage to detect the overall small-scale of movement revealed here.

Acknowledgements

We thank Dr Matt Taylor and two anonymous reviewers for constructive comments on earlier drafts of this manuscript. This study was funded by the New South Wales Saltwater Recreational Fishing Trust (NSW Research Angler Program – RFT Project No. DPI74) and the NSW Department of Primary Industries (NSW Gamefish Tagging Program).

References

Arlinghaus, R., Cooke, S., Lyman, J., Policansky, D., Schwab, A., Suski, C., . . . Thorstad, E. (2007). Understanding the Complexity of Catch-and-Release in Recreational Fishing: An Integrative Synthesis of Global Knowledge from Historical, Ethical, Social, and Biological Perspectives. *Reviews in Fisheries Science, 15*, 75-167. doi:10.1080/10641260601149432

Arnason, A. N., & Mills, K. H. (1981). Bias and Loss of Precision Due to Tag Loss in Jolly–Seber Estimates for Mark–Recapture Experiments. *Canadian Journal of Fisheries and Aquatic Sciences, 38*(9), 1077-1095. doi:10.1139/f81-148

Attwood, C. G., & Cowley, P. D. (2005). Alternate explanations of the dispersal pattern of galjoen *Dichistius capensis*. *African Journal of Marine Science, 27*(1), 141-156. doi:10.2989/18142320509504074

Bacheler, N. M., Paramore, L. M., Burdick, S. M., Buckel, J. A., & Hightower, J. E. (2009). Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. *Fishery Bulletin, 10*7(4), 405-419.

Bailey, K. M. (1997). Structural dynamics and ecology of flatfish populations. *Journal of Sea Research, 37*(3), 269-280. doi:https://doi.org/10.1016/S1385-1101(97)00018-X

Barnes, T., Junge, C., Myers, S., Taylor, M., Rogers, P., Ferguson, G., . . . Gillanders, B. (2015). Population structure in a wide-ranging coastal teleost (*Argyrosomus japonicus*, Sciaenidae) reflects marine biogeography across southern Australia. *Marine and Freshwater Research, 67*, 1103-1113. doi:10.1071/MF15044

Barnes, T. C, Rogers, P., Wolf, Y., Madonna, A., Holman, D., Ferguson, G., et al. (2019). Dispersal of an exploited demersal fish species (*Argyrosomus japonicus*, Sciaenidae) inferred from satellite telemetry. *Marine Biology*, *166*, 1-12.

Begg, G., & Waldman, J. (1999). An holistic approach to fish stock identification. *Fisheries Research, 43*, 35-44. doi:10.1016/S0165-7836(99)00065-X

Begg, G. A., Friedland, K. D., & Pearce, J. B. (1999). Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research, 43*(1), 1-8. doi:https://doi.org/10.1016/S0165-7836(99)00062-4

Boje, J. (2002). Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. *Fishery Bulletin, 100*, 414-422.

Brodie, S., Litherland, L., Stewart, J., Schilling, H. T., Pepperell, J. G., & Suthers, I. M. (2018). Citizen science records describe the distribution and migratory behaviour of a piscivorous predator, *Pomatomus saltatrix*. *ICES Journal of Marine Science, 75*(5), 1573-1582. doi:10.1093/icesjms/fsy057

Childs, A.-R., Cowley, P. D., Næsje, T. F. & Bennett, R. H. (2015). Habitat connectivity and intra-population structure of an estuary-dependent fishery species. Marine Ecology Progress Series, 537, 233-45. doi:https://doi.org/10.3354/meps11456

Comte, L., & Olden, J. (2018). Evidence for dispersal syndromes in freshwater fishes. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 2017-2214. doi:10.1098/rspb.2017.2214

Conroy, C. W., Piccoli, P. M., & Secor, D. H. (2015). Carryover effects of early growth and river flow on partial migration in striped bass *Morone saxatilis*. *Marine Ecology Progress Series, 541*, 179-194.

Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science, 1*(1), 443-466. doi:10.1146/annurev.marine.010908.163757

Cowley, P., Kerwath, S., Childs, A.-R., Thorstad, E., Økland, F., & Næsje, T. (2008). Estuarine habitat use by juvenile dusky kob *Argyrosomus japonicus* (Sciaenidae), with implications for management. *African Journal of Marine Science, 30*, 247-253. doi:10.2989/AJMS.2008.30.2.5.555

D'Anatro, A., Pereira, A., & Lessa, E. (2011). Genetic structure of the white croaker, *Micropogonias furnieri* Desmarest 1823 (Perciformes: Sciaenidae) along Uruguayan coasts: Contrasting marine, estuarine, and lacustrine populations. *Environmental Biology of Fishes, 91*, 407-420. doi:10.1007/s10641-011-9799-x

Domínguez-Petit, R., Korta, M., Saborido-Rey, F., Murua, H., Sainza, M., & Piñeiro, C. (2008). Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes. *Journal of Marine Systems, 71*(3), 260-278. doi:https://doi.org/10.1016/j.jmarsys.2007.04.004

Dunlop, S. W., Mann, B. Q., & van der Elst, R. P. (2013). A review of the Oceanographic Research Institute's Cooperative Fish Tagging Project: 27 years down the line. *African Journal of Marine Science, 35*(2), 209-221. doi:10.2989/1814232X.2013.769909

Earl, J., Fairclough, D., Staunton-Smith, J., Hughes, J., (2018). Mulloway *Argyrosomus japonicus*. In: Stewardson, C., Andrews, J., Ashby, C., Haddon, M., Hartmann, K., Hone, P., Horvat, P., Mayfield, S., Roelofs, A., Sainsbury, K., Saunders, T., Stewart, J., Nicol, S., Wise, B. (Eds.), *Status of Australian Fish Stocks Reports 2018*. Fisheries Research and Development Corporation, Canberra.

Edgar, G. J., Barrett, N. S., & Morton, A. J. (2004). Patterns of Fish Movement on Eastern Tasmanian Rocky Reefs. *Environmental Biology of Fishes, 70*(3), 273-284. doi:10.1023/B:EBFI.0000033342.89719.39

Espeland, S. H., Olsen, E. M., Knutsen, H., Gjøsæter, J., Danielssen, D. & Stenseth, N. C. (2008). New perspectives on fish movement: kernel and GAM smoothers applied to a century of tagging data on coastal Atlantic cod. *Marine Ecology Progress Series, 372,* 231-41. https://doi.org/10.3354/meps07721

Ferguson, G. J., Ward, T. M., & Geddes, M. C. (2008). Do recent age structures and historical catches of mulloway, *Argyrosomus japonicus* (Sciaenidae), reflect freshwater inflows in the remnant estuary of the Murray River, South Australia? *Aquat. Living Resour., 21*(2), 145-152. doi:https://doi.org/10.1051/alr:2008034

Ferguson, G. J., Ward, T. M., & Gillanders, B. M. (2011). Otolith shape and elemental composition: Complementary tools for stock discrimination of mulloway (*Argyrosomus japonicus*) in southern Australia. *Fisheries Research, 110*(1), 75-83. doi:https://doi.org/10.1016/j.fishres.2011.03.014

Ferguson, G. J., Ward, T. M., Ivey, A., & Barnes, T. (2014). Life history of *Argyrosomus japonicus*, a large sciaenid at the southern part of its global distribution: Implications for fisheries management. *Fisheries Research*, *151*, 148-157. doi:https://doi.org/10.1016/j.fishres.2013.11.002

Fowler, A. M., Smith, S. M., Booth, D. J., & Stewart, J. (2016). Partial migration of grey mullet (*Mugil cephalus*) on Australia's east coast revealed by otolith chemistry. *Marine Environmental Research, 119*, 238-244. doi:10.1016/j.marenvres.2016.06.010

Fowler, A. M., Chick, R. C., & Stewart, J. (2018). Patterns and drivers of movement for a coastal benthopelagic fish, *Pseudocaranx georgianus*, on Australia’s southeast coast. *Scientific Reports, 8*(1), 16738. doi:10.1038/s41598-018-34922-6

Fukumori, K., Okuda, N., Hamaoka, H., Fukumoto, T., Takahashi, D., & Omori, K. (2008). Stable isotopes reveal life history polymorphism in the coastal fish *Apogon notatus*. *Marine Ecology Progress Series, 362,* 279-289. doi:10.3354/meps07397

Gil, M. d. M., Palmer, M., Grau, A., Massutí, E., & Pastor, E. (2017). Comparing tagging strategies: Effects of tags on retention rate, mortality rate and growth in hatchery-reared juvenile meagre, *Argyrosomus regius* (Pisces: Sciaenidae). *Scientia Marina, 81*(2), 171-178. doi:10.3989/scimar.04583.26B

Gillanders, B., Ferrell, D., & Andrew, N. (2001). Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging programme? *Marine and Freshwater Research, 52,* 179-192.

Goethel, D., Quinn, T., & Cadrin, S. (2011). Incorporating Spatial Structure in Stock Assessment: Movement Modeling in Marine Fish Population Dynamics. *Reviews in Fisheries Science, 19,* 119-136. doi:10.1080/10641262.2011.557451

Gray, C. & McDonall, V. (1993). Distribution and growth of juvenile mulloway, *Argyrosomus hololepidotus* (Pisces: Sciaenidae), in the Hawkesbury River, south-eastern Australia. *Marine and Freshwater Research, 44,* 401-9. https://doi.org/10.1071/MF9930401

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., . . . White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews, 90*(4), 1215-1247. doi:https://doi.org/10.1111/brv.12155

Griffiths, M., & Hecht, T. (1995). Age and growth of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on otoliths. *South African Journal of Marine Science*, 119-128. doi:10.2989/025776195784156548

Griffiths, M. H. (1996). Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *South African Journal of Marine Science*, *17*(1), 135-154. doi:10.2989/025776196784158653

Griffiths, M. H., & Wilke, C. G. (2002). Long-term movement patterns of five temperate-reef fishes (Pisces : Sparidae): implications for marine reserves. *Marine and Freshwater Research, 53*(2), 233-244. doi:https://doi.org/10.1071/MF01148

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., & Botsford, L. W. (2011). Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation, 144*(2), 692-702. doi:https://doi.org/10.1016/j.biocon.2010.12.015

Hein, A. M., Hou, C., & Gillooly, J. F. (2012). Energetic and biomechanical constraints on animal migration distance. *Ecology Letters, 15*(2), 104-110. doi:https://doi.org/10.1111/j.1461-0248.2011.01714.x

Hilborn, R., Walters, C., & Jester Jr, D. (1990). *Value of fish marking in fisheries management.* Paper presented at the Prince, and GA Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium.

Hughes, J. M., Stewart, J., Gillanders, B. M., Collins, D., & Suthers, I. M. (2016). Relationship between otolith chemistry and age in a widespread pelagic teleost *Arripis trutta*: influence of adult movements on stock structure and implications for management. *Marine and Freshwater Research, 67*(2), 224-237. doi:https://doi.org/10.1071/MF14247

Hughes, J. M., Stewart, J., Lyle, J. M., McAllister, J., Stocks, J. R., & Suthers, I. M. (2017). Influence of latitudinal variation in environmental gradients and population structure on the demography of a widespread pelagic fish, *Arripis trutta* (Forster, 1801). *Environmental Biology of Fishes, 100*(2), 121-135. doi:10.1007/s10641-016-0565-y

Hughes, J. M., Stewart, J., & Collins, D. (2019). Simulated catch-and-release using experimental hyperbaric chamber trials reveal high levels of delayed mortality due to barotrauma in mulloway (*Argyrosomus japonicus*). *Journal of Experimental Marine Biology and Ecology, 516*, 89-102. doi:https://doi.org/10.1016/j.jembe.2019.05.001

Hutchins, B., & Swainston, R. (1986). *Sea fishes of southern Australia: complete field guide for anglers and divers*. Gary Allen Publishers.

Izzo, C., Ward, T. M., Ivey, A. R., Suthers, I. M., Stewart, J., Sexton, S. C., et al. (2018). Integrated approach to determining stock structure: implications for fisheries management of sardine, *Sardinops sagax*, in Australian waters. *Reviews in Fish Biology and Fisheries, 27*(1), 267-84. https://doi.org/10.1007/s11160-017-9468-z

Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., van Oppen, M. J. H., & Willis, B. L. (2009). Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs, 28*(2), 307-325. doi:10.1007/s00338-009-0469-9

Jonsson, B., & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries, 3*(4), 348-365. doi:10.1007/BF00043384

Kerr, L. A., Secor, D. H. & Piccoli, P. M. (2009). Partial Migration of Fishes as Exemplified by the Estuarine-Dependent White Perch. *Fisheries*, *34*(3), 114-23. https://doi.org/10.1577/1548-8446-34.3.114

Kritzer, J. P., & Sale, P. F. (2004). Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries, 5*(2), 131-140. doi:https://doi.org/10.1111/j.1467-2979.2004.00131.x

Kuiter, R. H. (1993). *Coastal fishes of south-eastern Australia*. University of Hawaii Press.

Kuparinen, A., Roney, N. E., Oomen, R. A., Hutchings, J. A., & Olsen, E. M. (2015). Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units. *ICES Journal of Marine Science, 73*(2), 286-292. doi:10.1093/icesjms/fsv181

Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology, 51*, 57-141. doi:10.1016/s0065-2881(06)51002-8

Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology, 19*(15), 3038-3051. doi:https://doi.org/10.1111/j.1365-294X.2010.04688.x

Lucy, J., & Davy, K. (2000). Benefits of Angler-assisted Tag and Release Programs. *Fisheries, 25*(4), 18-23. doi:10.1577/1548-8446(2000)025<0018:BOATAR>2.0.CO;2

Maggs, J., Cowley, P., Porter, S., & Childs, A.-R. (2019). Should I stay or should I go? Intra-population variability in movement behaviour of wide-ranging and resident coastal fishes. *Marine Ecology Progress Series, 619*, 111-124. doi:10.3354/meps12953

Mann, B. Q., Cowley, P. D. & Fennessy, S. T. (2015). Movement patterns of surf-zone fish species in a subtropical marine protected area on the east coast of South Africa. *African Journal of Marine Science, 37*(1), 99-114. https://doi.org/10.2989/1814232X.2015.1023220

Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models. *Computational Statistics & Data Analysis, 55*(7), 2372-2387. doi:https://doi.org/10.1016/j.csda.2011.02.004

Moore, B. R., Stapley, J., Allsop, Q., Newman, S. J., Ballagh, A., Welch, D. J., & Lester, R. J. G. (2011). Stock structure of blue threadfin *Eleutheronema tetradactylum* across northern Australia, as indicated by parasites. *Journal of Fish Biology, 78*(3), 923-936. doi:https://doi.org/10.1111/j.1095-8649.2011.02917.x

Morinville, G. R., & Rasmussen, J. B. (2006). Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy. *Journal of Animal Ecology, 75*(3), 693-704. doi:10.1111/j.1365-2656.2006.01090.x

Neira, F. J., Miskiewicz, A. G., & Trnski, T. (1998). *Larvae of temperate Australian fishes: laboratory guide for larval fish identification.* University of Western Australia Press.

Næsje, T. F., Cowley, P., Diserud, O., Childs, A.-R., Kerwath, S., & Thorstad, E. (2012). Riding the tide: Estuarine movements of a sciaenid fish, *Argyrosomus japonicus*. *Marine Ecology Progress Series, 460*, 221-232. doi:10.3354/meps09780

NSW DPI (2020). NSW DPI Gamefish Tagging Program Report 2018-2019. NSW Department of Primary Industries, NSW Government, Sydney.

Nøttestad, L., Giske, J., Holst, J. C., & Huse, G. (1999). A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences, 56*(S1), 26-34. doi:10.1139/f99-222

Pauly, D., Christensen, V., Guenette, S., Pitcher, T., Sumaila, R., Walters, C., . . . Zeller, D. (2002). Towards sustainability in world fisheries. *Nature, 418*, 689-695. doi:10.1038/nature01017

Ridgway, K. R., & Dunn, J. R. (2003). Mesoscale structure of the mean East Australian Current System and its relationship with topography. *Progress in Oceanography, 56*(2), 189-222. doi:https://doi.org/10.1016/S0079-6611(03)00004-1

Ridgway, K. R., & Godfrey, J. S. (1997). Seasonal cycle of the East Australian Current. *Journal of Geophysical Research: Oceans, 102*(C10), 22921-22936. doi:https://doi.org/10.1029/97JC00227

Rochford, D. (1984). Nitrates in eastern Australian coastal waters. *Marine and Freshwater Research, 35*(4), 385-397. doi:https://doi.org/10.1071/MF9840385

Secor, D. H. (1999). Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research, 43*(1), 13-34. doi:https://doi.org/10.1016/S0165-7836(99)00064-8

Silberschneider V., & Gray, C. A. (2005). Arresting the decline of the commercial and recreational fisheries for mulloway (*Argyrosomus japonicus*). *NSW DPI—Fisheries Final Report Series, 82*.

Silberschneider, V., & Gray, C. A. (2008). Synopsis of biological, fisheries and aquaculture-related information on mulloway *Argyrosomus japonicus* (Pisces: Sciaenidae), with particular reference to Australia. *Journal of Applied Ichthyology, 24*(1), 7-17. doi:https://doi.org/10.1111/j.1439-0426.2007.00913.x

Silberschneider, V., Gray, C., & Stewart, J. (2009). Age, growth, maturity and the overfishing of the iconic sciaenid, *Argyrosomus japonicus*, in south-eastern, Australia. *Fisheries Research, 95*, 220-229. doi:10.1016/j.fishres.2008.09.002

Smith, K. A. (2003). Larval distributions of some commercially valuable fish species over the Sydney continental shelf. *Proceedings of the Linnean Society of New South Wales, 124*, 1-11

Steffe, A. S., Macbeth, W. G., & Murphy, J. J. (2007). Status of the recreational fisheries in two Australian coastal estuaries following large fish-kill events. *Fisheries Research, 85*(3), 258-269. doi:https://doi.org/10.1016/j.fishres.2007.02.003

Stewart, J. (2011). Evidence of age-class truncation in some exploited marine fish populations in New South Wales, Australia. *Fisheries Research, 108*, 209-213. doi:10.1016/j.fishres.2010.11.017

Stewart, J., Hegarty, A., Young, C., Fowler, A., & Craig, J. (2015). Status of fisheries resources in NSW 2013–14. *NSW Department of Primary Industries, Sydney, NSW, Australia*.

Stewart, J., Pidd, A., Fowler, A. M., & Sumpton, W. (2019). Latitudinal variation in growth rates and limited movement patterns revealed for east-coast snapper *Chrysophrys auratus* through long-term cooperative-tagging programs. *Marine and Freshwater Research, 71*(6), 653-661. doi:https://doi.org/10.1071/MF19138

Suthers, I. M., Young, J. W., Baird, M. E., Roughan, M., Everett, J. D., Brassington, G. B., . . . Ridgway, K. (2011). The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. *Deep Sea Research Part II: Topical Studies in Oceanography, 58*(5), 538-546. doi:https://doi.org/10.1016/j.dsr2.2010.09.029

Takahashi, M., Okamura, H., Yokawa, K., & Okazaki, M. (2003). Swimming behaviour and migration of a swordfish recorded by an archival tag. *Marine and Freshwater Research, 54*(4), 527-534. doi:https://doi.org/10.1071/MF01245

Taylor, M. W., Laffan, S. D., Fielder, D., & Suthers, I. (2006). Key habitat and home range of mulloway *Argyrosomus japonicus* in a south-east Australian estuary: Finding the estuarine niche to optimise stocking. *Marine Ecology Progress Series, 328*, 237-247. doi:10.3354/meps328237

Taylor, M. D., van der Meulen, D. E., Ives, M. C., Walsh, C. T., Reinfelds, I. V., & Gray, C. A. (2014). Shock, Stress or Signal? Implications of Freshwater Flows for a Top-Level Estuarine Predator. *PLOS ONE, 9*(4), e95680. doi:10.1371/journal.pone.0095680

Taylor, M.D., Fowler, A.M. & Suthers, I.M. (2020). Insights into fish auditory structure–function relationships from morphological and behavioural ontogeny in a maturing sciaenid. *Marine Biology, 167,* 21. https://doi.org/10.1007/s00227-019-3619-9

West, L., Stark, K., Murphy, J., Lyle, J., & Ochwada-Doyle, F. (2015). Survey of recreational fishing in New South Wales and the ACT, 2013/14. *NSW DPI – Fisheries Final Report Series, 149.*

West, R., Thorogood, C., Walford, T., & Williams, R. (1985). An estuarine inventory for New South Wales, Australia. *Fisheries Bulletin 2, Department of Agriculture, Sydney.*

West R. J. (1992). Mulloway. The Australian Anglers Fishing World, August 1992. Yaffa Publishing Group, Sydney.

West R. J. (1993). Estuarine Fisheries Resources of two South-eastern Australian Rivers. Unpublished Ph.D Dissertation. The University of New South Wales.

Williams, A., Davies, C., Mapstone, B. D., & Russ, G. R. (2003). Scales of spatial variation in demography of a large coral-reef fish-an exception to the typical model? *Fishery Bulletin, 101,* 673-683.

Williams, A. J., Farley, J. H., Hoyle, S. D., Davies, C. R., & Nicol, S. J. (2012). Spatial and Sex-Specific Variation in Growth of Albacore Tuna (*Thunnus alalunga*) across the South Pacific Ocean. *PLOS ONE, 7*(6), e39318. doi:10.1371/journal.pone.0039318

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73*(1), 3-36. doi:https://doi.org/10.1111/j.1467-9868.2010.00749.x

Zarada, K., Walters Burnsed, S., Bickford, J., Ducharme-Barth, N., Ahrens, R. N. M. & Lowerre-Barbieri, S. (2019). Estimating site-specific spawning parameters for a spawning aggregation: an example with spotted seatrout. *Marine Ecology Progress Series, 624,* 117-29. https://doi.org/10.3354/meps13016

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution, 1*(1), 3-14. doi:https://doi.org/10.