# Latitudinal variation in growth rates and limited movement patterns revealed for east-coast snapper Chrysophrys auratus through long-term cooperative-tagging programs 

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#### Abstract

Understanding the spatial ecology of exploited fish stocks is key to their sustainable management. Here we used a long-term cooperative tag and recapture dataset that encompassed the entire distribution of the stock to examine patterns of movement and growth of Chrysophrys auratus (Sparidae) along eastern Australia. More than 24000 individuals were tagged, with 2117 being recaptured with information suitable for analysis of movements and 1440 with information suitable for analysis of growth rates. Individuals ranged in size between 120 - and $620-\mathrm{mm}$ fork length at tagging and were at liberty for up to 5.9 years before being recaptured. Results indicated population characteristics of partial migration, whereby the majority ( $\sim 71 \%$ ) of fish did not move any detectable distance and a small proportion $(\sim 4 \%)$ moved between 100 and 1000 km . Specific growth rates were significantly affected by the latitude at tagging, with higher growth rates at lower (more northern) latitudes. Our findings suggest that Australian east-coast C. auratus are mainly resident on a subdecadal time scale and at reasonably small spatial scales. When considered with information on latitudinal variation in growth and reproductive biology, localised recruitment and a history of localised fishery declines, assessment and management at local scales may be appropriate.


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## Introduction

Knowing how fish are distributed in space and time, and the demographic processes that drive these patterns, is important not only for sustainable fisheries management, but also for designing, implementing and interpreting biological and fishery assessments (Cooke et al. 2016). Broad-scale patterns of movement drive key aspects of the spatial ecology of exploited fish, including stock delineation, structure and mixing (Jacobsen and Hansen 2004; Cadrin et al. 2013; Izzo et al. 2017), and life history strategies (Montgomery 1990; Stewart and Kennelly 1998; Stewart et al. 2018). Understanding these general patterns of movements, including intraspecific variation (Parsons et al. 2011; Fowler et al. 2016) is requisite for determining appropriate spatial scales of monitoring, assessment and management (Ying et al. 2011; Cooke et al. 2016). In addition, studies into intraspecific variation in movement and behaviour are becoming increasingly important to fisheries management as evidence develops that many species exhibit partial migration, whereby both resident and migratory movement patterns occur within a single species (Parsons et al. 2011; Chapman et al. 2012; Fowler et al. 2016). Partial migration may have evolved to promote population stability (Chapman et al. 2006, 2011; Kerr et al.
2010) and ignoring it in management regimes may risk localised depletions and stock declines (Kerr et al. 2010; Parsons et al. 2011).

In addition to understanding the spatial ecology of fisheries, scientists and managers require information on population dynamics and key biological characteristics, such as growth and reproduction, and how these may vary spatially (Gertseva et al. 2017; Massie et al. 2018). Species that are distributed across a wide range of latitudes are likely to experience gradients in environmental conditions that directly influence life history traits (Stocks et al. 2015; Hughes et al. 2017). Latitudinal variation in environmental conditions, such as water temperature, habitat and food availability, can result in substantial differences in growth rates and productivity within fish populations (Hughes et al. 2013; Trip et al. 2014) that need to be accounted for in stock assessments and management plans. Indeed, without such information it may not be possible to determine appropriate scales of monitoring, assessment and management. Biologically inappropriate scales of management may result in risks to sustainability (Hutchinson 2008), localised depletions (Hanselman et al. 2007) or inefficient arrangements that limit productivity (Kerr et al. 2010).

Information on the range and extent of individual movements is essential for understanding the spatial ecology and demography of mobile species. Simple mark-recapture studies that record changes in the locations and sizes of fish between when they were tagged and recaptured have historically been used to study movements and growth. Such studies have been remarkably popular, with large-scale tagging programs being conducted at different places around world in an effort to study the biology and ecology of fish populations (Latour 2005). The use of external tags to study fish growth and movement patterns has diminished somewhat during the past decade or so with the development of acoustic tagging technology that can provide detailed information on individual fish behaviour (Nielsen et al. 2009; Thorstad et al. 2013). Such acoustic-tagging programs have provided important information for small-scale management, but may be limited by the expense of tagging and the upkeep of acoustic receivers, with the result being that studies are done on reasonably small numbers of individuals that are insufficient to characterise the broad-scale patterns often required for fisheries stock assessment and management (Taylor et al. 2017). It is therefore recognised that data from conventional external tag studies remain invaluable for informing assessment and management (Gillanders et al. 2001; Pine et al. 2003; Stewart et al. 2013).

Cooperative-tagging programs, in which research and government agencies work with recreational anglers who capture and tag fish and return the data to the management agency, have proven successful in providing data on growth rates, movements and habitat use (Gillanders et al. 2001; Stewart et al. 2013; Brodie et al. 2018). The long-term nature, widespread distribution and large numbers of tags used can overcome many of the shortcomings of such citizen science programs and provide important information on growth and movement patterns at scales that are relevant to fisheries management. Examining growth through tag-recapture methods provides a useful supplement to more common otolith-based investigations because it provides a direct and individualised assessment of change in body length per unit time. One such long-term (27 years) tag and recapture dataset exists for the Australian east-coast stock of snapper Chrysophrys auratus (Sparidae). Previously, a subset of these data was used to describe localised movements within a single embayment towards the northern end of its distribution (Sumpton et al. 2003); however, the combined dataset encompasses close to the entire distribution of this east-coast stock.
C. auratus are hugely important to commercial and recreational coastal fisheries (Paulin 1990; Parsons et al. 2014) and within Australia (Fowler et al. 2018a). Commonly referred to as snapper in the Southern Hemisphere, the species is distributed throughout the Indo-West Pacific region, Japan, Indonesia, southern Australia and New Zealand (Macdonald 1982; Henry and Gillanders 1999). In Australia, C. auratus are found in subtropical and temperate regions from Hinchinbrook Island in Queensland, throughout southern mainland Australian waters, to Barrow Island in Western Australia (Wakefield 2006). Juvenile C. auratus inhabit estuaries and shallow inshore waters, whereas adults aggregate in shelf waters generally between 20 and 60 m deep, but have been reported at depths of 200 m (Curley et al. 2013). A single east-coast biological stock of $C$. auratus occurs along eastern Australia down to
southern New South Wales (NSW), where some mixing occurs with the eastern Victorian stock (Fowler et al. 2018a; Morgan et al. 2019). Migratory dynamics within this stock are not well understood, with some studies reporting strong site fidelity, but with some individuals moving substantial distances and generally northwards (Sanders 1974; Sumpton et al. 2003; Harasti et al. 2015). Latitudinal variation in life history characteristics is also poorly understood across this stock; however, C. auratus are known to mature at smaller sizes and younger ages in more northern latitudes (Stewart et al. 2010), with spawning occurring earlier in the year towards the northern end of their distribution (Ferrell and Sumpton 1997). Latitudinal variation in growth rates in other populations of C. auratus in Australia and New Zealand has been reported (Jackson et al. 2010; Parsons et al. 2014). Currently, the east-coast biological stock of C. auratus is assessed as a single unit using an age-structured population model with biological parameters fixed for the entire stock (Wortmann et al. 2018). However, there is considerable debate around appropriate scales of assessment and management for this stock given long-term indications of localised depletions (Thurstan et al. 2018) and the lack of understanding of stock dynamics.

The aims of this study were to examine patterns in movement and growth within the Australian east-coast biological stock of C. auratus using a long-term tag and recapture dataset. Specifically, we investigated whether recaptured tagged fish had moved a detectable distance from their location of tagging given the spatial precision in the dataset. We then investigated the effects of latitude, direction of movement, days at liberty and body size at tagging on distance moved. The effect of latitude on growth rate was also examined and the results considered in terms of appropriate scales of assessment and management.

## Materials and methods

Data were available for $C$. auratus that were tagged between 1985 and 2011, from two major cooperative studies between the Queensland and NSW governments and recreational fishers, as well as various scientific studies. Both cooperative studies used single-barb spaghetti tags, with recreational fishers completing details on the date and location of tagging and fish length. Full details of the Queensland cooperative-tagging program with the Australian National Sportsfishing Association (ANSA) are detailed in Sumpton et al. (2003) and details of the NSW cooperative study in the NSW Gamefishing program are reported in Gillanders et al. (2001). In all, 24117 individual C. auratus were recorded as being tagged, with 17162 from the Queensland cooperative study, 674 from the NSW cooperative study and the remaining 6341 from various scientific projects run by the NSW government, with fish being tagged by scientists. Of these, 2117 fish were recaptured by fishers who provided appropriate recapture data.

## Data preparation

Data were checked before analysis and records that were missing key fields, such as dates, locations or fish lengths at tagging or recapture, were excluded. Records that had generic locations listed that could not be identified were also removed. Generic locations were assigned latitudes and longitudes at their
centres using Google Earth. Straight-line distances between tag and recapture locations were calculated using decimal latitudes and longitudes, and a predominant direction of movement, north or south, determined for each recapture event. Where fish lengths were reported as total lengths (TL) they were converted to fork lengths (FL) using the pre-established relationship:

$$
F L=0.83641 \times T L-0.49216
$$

where $r^{2}=0.99$.

## Movements

Recaptured C. auratus were assigned as having either moved from their location of tagging or not based on the distance between tag and recapture locations relative to the precision of those reported locations. The precision of reported locations was determined by the length of coastline bordering the location, as defined by council boundaries. For example, an individual with reported tagging and recapture locations of 'Coffs Harbour' would have registered no movement, despite the individual potentially moving up to 14 km (maximum length of the Coffs Harbour coastline). Precision estimates for reported locations ranged from 0.1 to 20 km , with $90 \%$ of individuals subject to precision of $<15 \mathrm{~km}$.
C. auratus that were deemed to have moved a detectable distance were further investigated using a generalised additive model (GAM) to examine whether distance moved (km; hereafter 'Distance') was affected by latitude of release (degrees; hereafter 'Latitude'), direction of movement (north or south; hereafter 'Direction'), days at liberty (hereafter 'Days') or body size at release (cm FL; hereafter 'Length'). The GAM approach was selected following preliminary data exploration that indicated potentially complex non-linear relationships between the response variable (Distance) and the continuous predictor variables. The gamma distribution with a log link was used owing to the positive continuous response variable and pattern of model residuals relative to that from an equivalent model using the normal distribution. Model improvement using the gamma distribution relative to the normal distribution was confirmed through comparison of Akaike information criterion (AIC) values.

Modelling was done using the gam function in the ' mgcv ' package (ver. 1.8-22, see https://cran.r-project.org/web/packages/ $\mathrm{mgcv} /$; Wood 2011) in R (ver. 3.4.4, R Foundation for Statistical Computing, Vienna, Austria). Smooth model terms were included for all continuous predictor variables, whereas Direction 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 towards infinity are penalised to zero and dropped from the model (Marra and Wood 2011). The upper limit to the effective degrees of freedom (e.d.f.) for smooth terms was initially set at $\mathrm{k}=10$ and the suitability of this choice was examined using the gam.check function to ensure e.d.f. were not overly restricted. The deviance explained by the final model was used to assess the quality of model fit.

Data were explored before 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 colinearity that occurs when a smooth term in a model could be approximated by one or more of the other smooth terms (Wood 2011).

## Growth rates

Latitudinal variation in growth performance was evaluated using the change in FL between tagging and recapture as a function of time at liberty for each individual available for these analyses. Growth performance was calculated in terms of specific growth rate (SGR; Lugert et al. 2016) as follows:
$S G R=\frac{\log (\text { length at recapture })-\log (\text { length at tagging })}{\text { Time at liberty }} \times 100$

A linear regression model was used to test the effect of latitude (in $1^{\circ}$ bands) at tagging on the SGR of individual C. auratus and was fitted using R (R Core Team Development Team). Individuals that had been at liberty for an insufficient time to exhibit detectable growth other than as a result of measurement error ( $<30$ days; see below) were excluded from these analyses following Ailloud et al. (2014) for tuna tagrecapture analyses.

Potential measurement error and bias in reported lengths at tagging and recapture (an important consideration in cooperative tagging studies; Gillanders et al. 2001) were investigated before analysis using records from fish that were at liberty for less than 30 days, the assumption being that measurable growth is likely to be negligible and centred at $\sim 0$ during that time (Gillanders et al. 2001; Stewart et al. 2013).

## Results

Following data checking, 2117 individual recapture records remained available for analysis of movements and 1439 remained available for analysis of growth rates. The data spanned $16^{\circ}$ latitude between 22 and $37^{\circ} \mathrm{S}$ (Fig. 1), and encompassed the entire distribution of the east-coast stock (Morgan et al. 2019). Days at liberty ranged between 1 and 2154 days ( 5.9 years), and straight line distances moved between 0 and 1133 km . The lengths of recaptured fish at tagging ranged between 120 and 620 mm FL.

## Movement

Of the 2117 individuals available for analysis of movements, 1502 ( $\sim 71 \%$ ) were deemed as having no detectable movement from their location of tagging. When accounting for the level of precision associated with 'zero' movers (see Materials and methods), $89.2 \%$ of individuals were recaptured within 20 km of their tagging location, and 54.1 and $47.0 \%$ were recaptured within 10 and 5 km respectively. C. auratus that had moved a detectable distance from their location of tagging did so with a median value of 9.9 km . Of those individuals that moved, $\sim 70 \%$ were recaptured within 25 km of where they were tagged and $\sim 80 \%$ were recaptured within 50 km , with 79 fish ( $<4 \%$ )
moving more than 100 km (Fig. 2). In total, 60\% of individuals that moved did so in a northerly direction.

For the 615 individuals that were assessed as having moved detectable distances from their locations of tagging, model selection retained the predictors Days, Latitude and Direction. The smooth term Length was penalised out of the model, with an e.d.f. approaching 0 (Fig. 3; Table 1). Days was a marginally significant predictor of Distance, with distance moved increasing linearly with days at liberty (Fig. 3), as indicated by an e.d.f. approaching 1 (Table 1). Greater movement was also predicted at higher relative to lower latitudes (Fig. 3); however, this effect was not significant at the $\alpha=0.05$ level (Table 1). A southerly


Fig. 1. Map of Australia's south-east coast indicating the proportion of releases (black bars) and recaptures (white bars) of Chrysophrys auratus at each degree of latitude. White lines on the map delineate state borders.
direction of movement (Direction - South) decreased the distance moved by a factor of 0.44 relative to northerly movements (Fig. 3; Table 1). Overall, the selected model explained only $21 \%$ of null deviance.

## Growth

Individual C. auratus that were recaptured within 30 days of tagging ( $n=347$ ) had a mean ( $\pm$ s.d.) change in length of $0.5 \pm 10.5 \mathrm{~cm}$, suggesting some measurement errors within the dataset but with no bias (Fig. 4). Therefore, the dataset was considered suitable for the analysis of growth rates.

Individual SGRs ranged between 0 and 0.7 (mean $=0.02$ ). SGR was significantly affected by the latitude at tagging (Table 2). The coefficients for latitude were negative, indicating a declining trend in SGR with increasing latitude. Average absolute growth rates peaked at $\sim 50 \mathrm{~mm}$ year ${ }^{-1}$ for fish averaging $300-350 \mathrm{~mm}$ FL between tagging and recapture (Table 3).

## Discussion

Results from the long-term tagging and recapture dataset encompassing the entire distribution of the east-coast stock for C. auratus confirm and extend the findings of previous studies on parts of the stock done at reasonably small spatial scales (Sumpton et al. 2003; Harasti et al. 2015). In fact, the citizen science aspect of this cooperative-tagging program enabled analyses at temporal and spatial scales rarely achieved through fishery-independent studies. East-coast C. auratus are characterised as being primarily resident over relatively small spatial (tens of kilometres) and decadal time scales, with a small percentage of individuals moving considerable distances (up to $1000 \mathrm{~km})$. This partial migration, whereby both resident and migratory movement patterns occur within a single species, is thought to convey population resilience and has been reported in various teleosts (Fowler et al. 2016, 2018b), including C. auratus from New Zealand (Parsons et al. 2011, 2014). The drivers for determining which individual C. auratus decide to migrate large distances while their conspecifics remain resident


Fig. 2. Distribution of distances moved for Chrysophrys auratus that were deemed as having moved detectable distances from their locations of tagging $(n=615)$.
are not known; however, they may relate to genetics or environmental factors. Parsons et al. (2011) found ontogeny unlikely to be a factor, which was supported by our finding that fish length at tagging did not have a major effect on the distance moved, and hypothesised that interactions between habitat quality and population density may be important, with higher physiological performance achieved through movement away from over-populated habitats. For example, structurally complex rocky reef habitats may be more suitable for residency at higher densities through provision of greater food resources and shelter (Parsons et al. 2011). Exploitation rates and potential fishery-induced selection further complicate the development of models to explain the dynamics of partial migration, and further work is clearly needed to better understand the phenomenon in the Australian east-coast C. auratus stock. Whatever the drivers behind some individuals moving long distances, it is these individuals that likely perpetuate the single genetic stock along the east coast of Australia, because modelling of larval trajectories suggests limited dispersal (Roughan et al. 2011; Curley et al. 2013).
C. auratus that exhibited detectable movement away from their locations of tagging generally did not move far, with a median distance of just 9.9 km , noting that these estimations were minima because individuals likely moved further than the straight line distances between tagging and recapture locations. Individuals that did move were more likely to do so in a
northerly direction and to move greater distances than those individuals that travelled southwards. It has been hypothesised that some east-coast C. auratus may participate in a prespawning migration northwards (Harasti et al. 2015), but this has not been confirmed. Such a phenomenon has been reported in New Zealand, whereby some C. auratus form highly mobile groups that travel long distances to spawn (Parsons et al. 2014). The prevailing currents along eastern Australia are southerly flowing via the Eastern Australian Boundary Current (Ridgway and Dunn 2003), and many coastal species migrate northwards to

Table 1. Model results for the generalised additive model of Chrysophrys auratus movements
Values in parentheses are $95 \%$ confidence limits around the parametric estimate. The parametric estimate is back-transformed from the modelled (log) scale. s( $\ldots$ ), smooth terms; $\beta$, effective degrees of freedom (degree of non-linearity) for smoother terms and the coefficient estimate for the parametric term Direction - South; FL, fork length

| Model term | Covariate range | $\beta$ | $P$-value |
| :--- | :---: | :--- | ---: |
| $s$ (Length) | $15.0-53.5 \mathrm{~cm} \mathrm{FL}$ | 0.000 | 0.77 |
| $s$ (Days) | $0-999$ | 0.851 | 0.04 |
| $s$ (Latitude) | $25.3-34.1^{\circ} \mathrm{S}$ | 1.375 | 0.09 |
| Direction - South | - | $0.437(0.596-0.230)$ | $<0.01$ |



Fig. 3. Partial effects of smooth terms and the parametric term Direction for the generalised additive model of Chrysophrys auratus movement. The $y$-axis values are the contribution of the smoother to the model's fitted values. Solid lines represent the model estimates; shaded regions and dashed lines indicate $95 \%$ confidence intervals. Length is fork length in millimetres and latitude is degrees south. The values for Direction are on the modelled (log) scale.


Fig. 4. Change in length of tagged Chrysophrys auratus that were recaptured within 30 days of release.

Table 2. Linear regression model outputs for the growth performance (specific growth rate) of Chrysophrys auratus $200-250 \mathrm{~mm}$ fork length (FL) when tagged, and all individuals, against each $1^{\circ}$ of latitude at tagging

| Length at tagging | Coefficient | Estimate | s.e. | $P$-value |
| :--- | :--- | ---: | :---: | :---: |
| 200-250 mm FL | Intercept | 0.0900481 | 0.0117158 | $<0.001$ |
|  | Latitude | -0.0023698 | 0.0004121 | $<0.001$ |
| All | Intercept | 0.0875739 | 0.0085175 | $<0.001$ |
|  | Latitude | -0.0023181 | 0.0003083 | $<0.001$ |

Table 3. Specific growth rate (SGR) and absolute growth rate for Chrysophrys auratus by mean fork length (mean of lengths at tagging and recapture)
Data are the mean $\pm$ s.e.m. Only size classes with more than five observations are included

| Fork length $(\mathrm{mm})$ | SGR | Growth rate $\left(\mathrm{mm} \mathrm{year}^{-1}\right)$ |
| :--- | ---: | :---: |
| 175 | $0.009 \pm 0.006$ | $12.521 \pm 8.398$ |
| 225 | $0.0209 \pm 0.002$ | $36.236 \pm 3.031$ |
| 275 | $0.0228 \pm 0.001$ | $47.037 \pm 2.217$ |
| 325 | $0.0203 \pm 0.002$ | $49.611 \pm 3.719$ |
| 375 | $0.008 \pm 0.002$ | $22.693 \pm 5.164$ |
| 425 | $0.0089 \pm 0.003$ | $29.925 \pm 8.761$ |
| 475 | $0.0067 \pm 0.003$ | $26.142 \pm 10.354$ |

spawn, potentially so that eggs and larvae are transported southwards to suitable habitat (Montgomery 1990; Stewart and Kennelly 1998; Virgona et al. 1998). The spawning dynamics of east-coast C. auratus are not well understood, and more research is required to identify the existence of any such migratory pattern along eastern Australia and its potential importance to the stock.

One limitation within the present tag and recapture dataset is that the sizes and locations of each individual are only available at two points in time, the dates of tagging and recapture, with no information on where the fish were between these times. Therefore, it may have been possible for individuals to move considerable distances after being tagged, only to return to their approximate locations of tagging before being recaptured. Given the multidecadal nature of the study across the entire distribution of the Australian east-coast stock, we think it unlikely that any such consistent migration pattern would go undetected; however, the untested northwards prespawning migration hypothesis of Harasti et al. (2015) and the knowledge gaps surrounding spawning dynamics described above should be researched using alternative techniques to those used here. Finer-scale resolution of movement patterns and stock dynamics within Australian populations of C. auratus have been reported using techniques such as acoustic tagging (Harasti et al. 2015; Fowler et al. 2017a), otolith chemistry (Hamer et al. 2011; Fowler et al. 2017b) and integration of tagging data with patterns in biology and life history (Coutin et al. 2003).

Our findings that east-coast C. auratus are largely resident do support the growing body of literature that individuals of this species benefit from no-take marine reserves (Harasti et al. 2015). Studies into marine protected areas (MPAs) in NSW have demonstrated increases in both the relative abundance and size of C. auratus within no fishing zones (Malcolm et al. 2015, 2018; Harasti et al. 2018a, 2018b) which is not surprising given the majority of individuals do not move far. However, the importance of such no-take MPAs to overall stock status and the fisheries that exploit C. auratus is questionable, given any spillover into fishable areas may be minor in terms of exploitable-sized individuals and new recruits (Roughan et al. 2011). However, if the hypothesis of Parsons et al. (2011) applies to Australian east-coast C. auratus, and a driver for individuals to migrate is related to the productivity and carrying capacity of habitat, then, as the populations increase within no fishing areas, the partial migration strategy identified during the
present study may, in fact, increase the benefits of spillover from these areas. More targeted research into the behaviour of individual C. auratus within MPAs and whether it varies with population density would help our understanding of the benefits of MPAs to the overall stock and fisheries for east-coast C. auratus. This spillover effect is thought to be a major driver of population dynamics for the western Victorian stock (Hamer et al. 2011; Fowler et al. 2017b).

We have demonstrated, for the first time, that growth rates of Australian east-coast C. auratus vary with latitude, with faster growth rates being detected at more northern latitudes. Growth rates in teleosts, including sparids, have often been linked to water temperature, with warmer waters resulting in increased metabolic rates and faster growth (Sarre and Potter 2000; Stocks et al. 2011; Morrongiello and Thresher 2015). Given our finding that east-coast $C$. auratus are largely resident, and that average annual water temperatures vary considerably along the eastcoast of Australia, with more northern latitudes experiencing higher temperatures (Suthers et al. 2011), our findings are perhaps not surprising. Nevertheless, the spatial variation in growth rates identified here supports the restricted movement observed from the tagging component of the study, because latitudinal variation in demographic rates would not be possible if individuals were fully mixed throughout their range. Furthermore, the spatial variation in growth rates confirms that restricted movement has demographic consequences for the productivity of the east-coast snapper stock: southern individuals produce exploitable biomass more slowly than conspecifics in the north. Similar trends of increasing growth rates with decreasing latitude have been reported in other populations of C. auratus from Australia and New Zealand (Jackson et al. 2010), noting that population density may confound this general pattern (Parsons et al. 2014).

## Implications for assessment and management

Despite being considered and assessed as a single biological stock (Wortmann et al. 2018; Morgan et al. 2019), there is growing evidence that east-coast $C$. auratus should be assessed and managed at a more local scale. Our findings that east-coast C. auratus are primarily resident with limited mixing within the stock support this. Significant latitudinal variation in key biological traits such as growth, as demonstrated in the present study, as well as the size and age at sexual maturity and spawning season (Stewart et al. 2010) suggest that the productivity of the stock will vary substantially across its range and should be taken into account in future stock assessments and potentially management regulations. It is reported that larvae are likely to recruit locally (Roughan et al. 2011; Curley et al. 2013) and that the majority of the offshore catch is derived from only a subset of local estuaries (Gillanders 2002). These characteristics are consistent with the long history of reported localised depletions across this stock (Thurstan et al. 2018) and suggest that future assessment and management at reasonably small spatial scales may be required to sustain local fisheries.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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## References

Ailloud, L. E., Lauretta, M. V., Hoenig, J. M., Walter, J. F., and Fonteneau, A. (2014). Growth of Atlantic bluefin tuna determined from the ICCAT tagging database: a reconsideration of methods. Collective Volume of Scientific Papers 70(2), 380-393.
Brodie, S., Litherland, L., Stewart, J., Schilling, H. T., Pepperell, J. G., and 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
Cadrin, S. X., Kerr, L. A., and Mariani, S. (Eds) (2013). 'Stock Identification Methods: Applications in Fishery Science.' (Academic Press: Waltham, MA, USA.)
Chapman, A., Morgan, D. L., Beatty, S. J., and Gill, H. S. (2006). Variation in life history of land-locked lacustrine and riverine populations of Galaxias maculatus (Jenyns 1842) in Western Australia. Environmental Biology of Fishes 77, 21-37. doi:10.1007/S10641-006-9051-2
Chapman, B. B., Brönmark, C., Nilsson, J. A., and Hansson, L. A. (2011). The ecology and evolution of partial migration. Oikos $\mathbf{1 2 0}(12), 1764$ 1775. doi:10.1111/J.1600-0706.2011.20131.X

Chapman, B. B., Hulthen, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L. A., and Brönmark, C. (2012). Partial migration in fishes: causes and consequences. Journal of Fish Biology 81, 456-478. doi:10.1111/J.1095-8649.2012.03342.X
Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F., Power, M., Doka, S. E., Dettmers, J. M., Crook, D. A., Lucas, M. C., Holbrook, C. M., and Krueger, C. C. (2016). A moving target - incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. Environmental Monitoring and Assessment 188(4), 239. doi:10.1007/S10661-016-5228-0
Coutin, P. C., Cashmore, S., and Sivakumuran, K. P. (2003). Assessment of the snapper fishery in Victoria. Project number 97/127, final report to Fisheries Research and Development Corporation, Australia, Department of Primary Industries, Queenscliff, Vic., Australia.
Curley, B. G., Jordan, A. R., Figueira, W. F., and Valenzuela, V. C. (2013). A review of the biology and ecology of key fishes targeted by coastal fisheries in south-east Australia: identifying critical knowledge gaps required to improve spatial management. Reviews in Fish Biology and Fisheries 23(4), 435-458. doi:10.1007/S11160-013-9309-7
Ferrell, D. J., and Sumpton, W. D. (1997). Assessment of the fishery for snapper (Pagrus auratus) in Queensland and New South Wales. Report to the Fisheries Research and Development Corporation, Project 93/074, Queensland Department of Primary Industries and the New South Wales Fisheries Research Institute, Canberra, ACT, Australia.
Fowler, A. M., Smith, S. M., Booth, D. J., and 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. J., Huveneers, C., and Lloyd, M. T. (2017a). Insights into movement behaviour of snapper (Chrysophrys auratus, Sparidae) from a large acoustic array. Marine and Freshwater Research 68, 1438-1453. doi:10.1071/MF16121

Fowler, A. J., Hamer, P. A., and Kemp, J. (2017b). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely dispersed, coastal fishery species. Fisheries Research 189, 77-94. doi:10.1016/J.FISHRES.2017.01.010
Fowler, A., Jackson, G., Stewart, J., Hamer, P., and Roelofs, A. (2018a). Snapper (Pagrus auratus). In 'Status of Australian Fish Stocks Reports 2018'. (Eds C. Stewardson, J. Andrews, C. Ashby, M. Haddon, K. Hartmann, P. Hone, P. Horvat, S. Mayfield, A. Roelofs, K. Sainsbury, T. Saunders, J. Stewart, S. Nicol, and B. Wise.) (Fisheries Research and Development Corporation: Canberra, ACT, Australia.)
Fowler, A. M., Chick, R. C., and Stewart, J. (2018b). Patterns and drivers of movement for a coastal benthopelagic fish, Pseudocaranx georgianus, on Australia's south-east coast. Scientific Reports 8(1), 16738. doi:10. 1038/S41598-018-34922-6
Gertseva, V., Matson, S. E., and Cope, J. (2017). Spatial growth variability in marine fish: example from north-east Pacific groundfish. ICES Journal of Marine Science 74(6), 1602-1613. doi:10.1093/ICESJMS/FSX016
Gillanders, B. M. (2002). Connectivity between juvenile and adult fish populations: do adults remain near their recruitment estuaries? Marine Ecology Progress Series 240, 215-223. doi:10.3354/MEPS240215
Gillanders, B. M., Ferrell, D. J., and Andrew, N. L. (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(2), 179-192. doi:10.1071/ MF99153
Hamer, P. A., Acevedo, S., Jenkins, G. P., and Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78, 1090-1109. doi:10.1111/J.1095-8649. 2011.02921.X

Hanselman, D., Spencer, P., Shotwell, K., and Reuter, R. (2007). Localised depletion of three Alaska rockfish species. In 'Biology, Assessment, and Management of North Pacific Rockfishes'. (Eds J. Heifitz, J. Dicosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley.) Alaska Sea Grant College Program Report, pp. 493-511. (University of Alaska-Fairbanks: Fairbanks, AK, USA.)
Harasti, D., Lee, K. A., Gallen, C., Hughes, J. M., and Stewart, J. (2015). Movements, home range and site fidelity of snapper (Chrysophrys auratus) within a no-take marine protected area. PLoS One 10(11), e0142454. doi:10.1371/JOURNAL.PONE. 0142454
Harasti, D., Williams, J., Mitchell, E., Lindfield, S., and Jordan, A. (2018a). Increase in relative abundance and size of snapper Chrysophrys auratus within partially protected and no-take areas in a temperate marine protected area. Frontiers in Marine Science 5, 208. doi:10.3389/ FMARS.2018.00208
Harasti, D., Davis, T. R., Mitchell, E., Lindfield, S., and Smith, S. D. (2018b). A tale of two islands: decadal changes in rocky reef fish assemblages following implementation of no-take marine protected areas in New South Wales, Australia. Regional Studies in Marine Science 18, 229-236. doi:10.1016/J.RSMA.2017.10.011
Henry, G., and Gillanders, B. (1999). Snapper and yellowtail kingfish. In 'Under Southern Seas: The Ecology of Australia's Rocky Reefs'. (Ed. N. Andrew.) pp. 158-171. (University of New South Wales Press: Sydney, NSW, Australia.)
Hughes, J. M., Stewart, J., Lyle, J. M., McAllister, J., Stocks, J. R., and Suthers, I. M. (2013). Latitudinal, ontogenetic, and historical shifts in the diet of a carnivorous teleost, Arripis trutta, in a coastal pelagic ecosystem altered by climate change. Canadian Journal of Fisheries and Aquatic Sciences 70(8), 1209-1230. doi:10.1139/CJFAS-2013-0083
Hughes, J. M., Stewart, J., Lyle, J. M., McAllister, J., Stocks, J. R., and 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

Hutchinson, W. F. (2008). The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. Biology Letters 4(6), 693-695. doi:10.1098/RSBL.2008.0443
Izzo, C., Ward, T. M., Ivey, A. R., Suthers, I. M., Stewart, J., Sexton, S. C., and Gillanders, B. M. (2017). 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), 267-284. doi:10.1007/S11160-017-9468-Z
Jackson, G., Norriss, J. V., Mackie, M. C., and Hall, N. G. (2010). Spatial variation in life history characteristics of snapper (Pagrus auratus) within Shark Bay, Western Australia. New Zealand Journal of Marine and Freshwater Research 44(1), 1-15. doi:10.1080/00288331003641646
Jacobsen, J. A., and Hansen, L. P. (2004). Conventional tagging methods in stock identification: internal and external tags. ICES ASC 2004/EE:29. Available at http://www.hav.fo/PDF/Ritgerdir/2004/ICES_CM2004_EE29. pdf [Verified 8 August 2019].
Kerr, L. A., Cadrin, S. X., and Secor, D. H. (2010). The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecological Applications 20(2), 497-507. doi:10.1890/ 08-1382.1
Latour, R. J. (2005). Tagging methods and associated data analysis. FAO Fisheries Technical Paper 474, 45-61.
Lugert, V., Thaller, G., Tetens, J., Schulz, C., and Krieter, J. (2016). A review on fish growth calculation: multiple functions in fish production and their specific application. Reviews in Aquaculture 8(1), 30-42. doi:10.1111/RAQ. 12071
Macdonald, C. M. (1982). Life history characteristics of snapper Chrysophrys auratus (Bloch and Schneider, 1801) in Australian waters. Fisheries and Wildlife Paper, Victoria, 29, Ministry for Conservation Fisheries and Wildlife Division, Melbourne, Vic., Australia.
Malcolm, H. A., Schultz, A. L., Sachs, P., Johnstone, N., and Jordan, A. (2015). Decadal changes in the abundance and length of snapper (Chrysophrys auratus) in subtropical marine sanctuaries. PLoS One 10(6), e0127616. doi:10.1371/JOURNAL.PONE. 0127616
Malcolm, H. A., Williams, J., Schultz, A. L., Neilson, J., Johnstone, N., Knott, N. A., Harasti, D., Coleman, M. A., and Jordan, A. (2018). Targeted fishes are larger and more abundant in 'no-take' areas in a subtropical marine park. Estuarine, Coastal and Shelf Science 212, 118-127. doi:10.1016/J.ECSS.2018.07.003
Marra, G., and Wood, S. N. (2011). Practical variable selection for generalized additive models. Computational Statistics \& Data Analysis 55, 2372-2387. doi:10.1016/J.CSDA.2011.02.004
Massie, D. L., Smith, G. D., Bonvechio, T. F., Bunch, A. J., Lucchesi, D. O., and Wagner, T. (2018). Spatial variability and macro-scale drivers of growth for native and introduced flathead catfish populations. Transactions of the American Fisheries Society 147(3), 554-565. doi:10.1002/ TAFS. 10055
Montgomery, S. S. (1990). Movements of juvenile eastern king prawns, Penaeus plebejus, and identification of stock along the east coast of Australia. Fisheries Research 9(3), 189-208. doi:10.1016/S0165-7836(05)80001-3
Morgan, J. A., Sumpton, W. D., Jones, A. T., Campbell, A. B., Stewart, J., Hamer, P., and Ovenden, J. R. (2019). Assessment of genetic structure among Australian east coast populations of snapper Chrysophrys auratus (Sparidae). Marine and Freshwater Research 70(7), 964-976. doi:10.1071/MF18146
Morrongiello, J. R., and Thresher, R. E. (2015). A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. Ecological Monographs 85, 93-115. doi:10.1890/13-2355.1
Nielsen, J. L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M., and Sibert, J. (2009). 'Tagging and Tracking of Marine Animals with Electronic Devices, Vol. 9.' (Springer Science \& Business Media: Berlin, Germany.)

Parsons, D. M., Morrison, M. A., McKenzie, J. R., Hartill, B. W., Bian, R., and Francis, R. C. (2011). A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (Pagrus auratus). Canadian Journal of Fisheries and Aquatic Sciences 68(4), 632-642. doi:10.1139/F2011-005
Parsons, D. M., Sim-Smith, C. J., Cryer, M., Francis, M. P., Hartill, B., Jones, E. G., Le Port, A., Lowe, M., McKenzie, J., Morrison, M., and Paul, L. J. (2014). Snapper (Chrysophrys auratus): a review of life history and key vulnerabilities in New Zealand. New Zealand Journal of Marine and Freshwater Research 48(2), 256-283. doi:10.1080/00288330.2014. 892013
Paulin, C. D. (1990). Pagrus auratus, a new combination for the species known as snapper in Australasian waters (Pisces: Sparidae). New Zealand Journal of Marine and Freshwater Research 24, 259-265. doi:10.1080/00288330.1990.9516422
Pine, W. E., Pollock, K. H., Hightower, J. E., Kwak, T. J., and Rice, J. A. (2003). A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28(10), 10-23. doi:10.1577/ 1548-8446(2003)28[10:AROTMF]2.0.CO;2
Ridgway, K. R., and Dunn, J. R. (2003). Mesoscale structure of the mean East Australian Current System and its relationship with topography. Progress in Oceanography 56, 189-222. doi:10.1016/S0079-6611(03)00004-1
Roughan, M., Macdonald, H. S., Baird, M. E., and Glasby, T. M. (2011). Modelling coastal connectivity in a Western Boundary Current: Seasonal and inter-annual variability. Deep-sea Research - II. Topical Studies in Oceanography 58(5), 628-644. doi:10.1016/J.DSR2.2010. 06.004

Sanders, M. J. (1974). Tagging indicates at least two stocks of snapper Chrysophrys auratus in south-east Australian waters. New Zealand Journal of Marine and Freshwater Research 8(2), 371-374. doi:10. 1080/00288330.1974.9515511
Sarre, G. A., and Potter, I. C. (2000). Variation in age compositions and growth rates of Acanthopagrus butcheri (Sparidae) among estuaries: some possible contributing factors. Fishery Bulletin 98, 785-799.
Stewart, J., and Kennelly, S. J. (1998). Contrasting movements of two exploited Scyllarid lobsters of the genus Ibacus off the east coast of Australia. Fisheries Research 36, 127-132. doi:10.1016/S0165-7836(98)00104-0
Stewart, J., Rowling, K., Hegarty, A.-M., and Nuttall, A. (2010). Size and age at sexual maturity of snapper Pagrus auratus in New South Wales 2008/09. Fisheries Research Report Series number 27, Industry \& Investment NSW, Sydney, NSW, Australia.
Stewart, J., Robbins, W. D., Rowling, K., Hegarty, A., and Gould, A. (2013). A multifaceted approach to modelling growth of the Australian bonito Sarda australis (Family Scombridae). Journal of Fish Biology 64, 671-678.
Stewart, J., Hegarty, A., Young, C., and Fowler, A. M. (2018). Genderspecific differences in growth, mortality and migration support population resilience in a heavily exploited migratory marine teleost, Mugil cephalus (Linnaeus 1758). Marine and Freshwater Research 69, 385-394. doi:10.1071/MF17135
Stocks, J., Stewart, J., Gray, C. A., and West, R. J. (2011). Using otolith increment widths to infer spatial, temporal and gender variation in the growth of sand whiting Sillago ciliata. Fisheries Management and Ecology 18, 121-131. doi:10.1111/J.1365-2400.2010.00761.X
Stocks, J. R., Gray, C. A., and Taylor, M. D. (2015). Intra-population trends in the maturation and reproduction of a temperate marine herbivore

Girella elevata across latitudinal clines. Journal of Fish Biology 86(2), 463-483. doi:10.1111/JFB. 12563
Sumpton, W. D., Sawynok, B., and Carstens, N. (2003). Localised movement of snapper (Pagrus auratus, Sparidae) in a large subtropical marine embayment. Marine and Freshwater Research 54(8), 923-930. doi:10. 1071/MF02119
Suthers, I. M., Everett, J. D., Roughan, M., Young, J. W., Oke, P. R., Condie, S. A., Hartog, J. R., Hobday, A. J., Thompson, P. A., Ridgway, K., Baird, M. E., Hassler, C. S., Brassington, G. B., Byrne, M., Holbrook, N. J., and Malcolm, H. A. (2011). The strengthening East Australian Current, its eddies and biological effects - an introduction and overview. Deep-sea Research - II. Topical Studies in Oceanography 58, 538-546. doi:10. 1016/J.DSR2.2010.09.029
Taylor, M. D., Babcock, R. C., Simpfendorfer, C. A., and Crook, D. A. (2017). Where technology meets ecology: acoustic telemetry in contemporary Australian aquatic research and management. Marine and Freshwater Research 68(8), 1397-1402. doi:10.1071/MF17054
Thorstad, E. B., Rikardsen, A. H., Alp, A., and Økland, F. (2013). The use of electronic tags in fish research - an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13(5), 881-896.
Thurstan, R. H., Buckley, S. M., and Pandolfi, J. M. (2018). Trends and transitions observed in an iconic recreational fishery across 140 years. Global Environmental Change 52, 22-36. doi:10.1016/J.GLOENV CHA.2018.06.002
Trip, E. D., Clements, K. D., Raubenheimer, D., and Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. Journal of Animal Ecology 83(4), 866-875. doi:10.1111/1365-2656.12183
Virgona, J., Deguara, K., Sullings, D., Halliday, I., and Kelly, K. (1998). 'Assessment of the Stocks of Sea Mullet in New South Wales and Queensland Waters.' (NSW Fisheries Research Institute: Sydney, NSW, Australia.)
Wakefield, C. B. (2006). Latitudinal and temporal comparisons of the reproductive biology and growth of snapper, Pagrus auratus (Sparidae), in Western Australia. Ph.D. Thesis, Murdoch University, Perth, WA, Australia.
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:10.1111/J.1467-9868.2010.00749.X
Wortmann, J., O’Neill, M. F., Sumpton, W., and Stewart, J. (2018). Stock assessment of Australian east coast snapper, Chrysophrys auratus. Predictions of stock status and reference points for 2016. Technical Report. (Department of Agriculture and Fisheries, State of Queensland.) Available at http://era.daf.qld.gov.au/id/eprint/6341/[Verified 8 August 2019].
Ying, Y., Chen, Y., Lin, L., and Gao, T. (2011). Risks of ignoring fish population spatial structure in fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 68(12), 2101-2120. doi:10.1139/ F2011-116
Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1, 3-14. doi:10.1111/J.2041-210X.2009.00001.X

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