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# 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 24 000 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-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 (~71%) of fish did not move any detectable distance and a small proportion (~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.

Additional keywords: fisheries, life history, partial migration.

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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.* 2018*a*). 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:

$$FL = 0.83641 \times TL - 0.49216$$

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 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/ 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 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:

$$SGR = \frac{\log(\text{length at recapture}) - \log(\text{length at tagging})}{\text{Time at liberty}} \times 100$$

A linear regression model was used to test the effect of latitude (in 1° 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 tag–recapture 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  $37^{\circ}$ 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 (±s.d.) change in length of  $0.5 \pm 10.5$  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 mm year<sup>-1</sup> for fish averaging 300–350 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 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(...), 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	β	P-value
s(Length)	15.0–53.5 cm FL	0.000	0.77
s(Days)	0-999	0.851	0.04
s(Latitude)	25.3–34.1°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 mm fork length(FL) when tagged, and all individuals, against each 1° of latitude at<br/>tagging

Length at tagging	Coefficient	Estimate	s.e.	P-value
200–250 mm FL	Intercept	0.090 048 1	0.011 715 8	<0.001
	Latitude	-0.002 369 8	0.000 412 1	<0.001
All	Intercept	0.087 573 9	0.008 517 5	<0.001
	Latitude	-0.002 318 1	0.000 308 3	<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 (mm)	SGR	Growth rate (mm year $^{-1}$ )
175	$0.009\pm0.006$	$12.521 \pm 8.398$
225	$0.0209\pm0.002$	$36.236 \pm 3.031$
275	$0.0228\pm0.001$	$47.037 \pm 2.217$
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	$0.0067\pm0.003$	$26.142 \pm 10.354$

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.* 2017*b*).

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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