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Does a spatio-temporal closure to fishing *Chrysophrys auratus* (Sparidae) spawning aggregations also protect individuals during migration?

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Abstract

Understanding migration dynamics of fishes that aggregate-spawn is critical if spatio-temporal closures to fishing are expected to protect them. Concern over fishing of *Chrysophrys auratus* spawning aggregations in embayments near a west Australian city led to an annual four-month spatial fishing closure. However, the extent to which it protects fish migrating to and from aggregations is unclear. Acoustic telemetry demonstrated a bimodal pattern of entry to and departure from the main embayment via only one of several pathways. Among years, 33-56% of fish occurred in the pathway prior to the closure, but most left before it ceased. Fish were detected within the closure in multiple but not always consecutive years. Variation in migration timing and aggregation philopatry may alter capture risk, but pre- and post-spawning migratory fish are fished in the main pathway and adjacent reefs, which would presumably impact spawning aggregation biomass. Assessment of this would assist in understanding whether expansion of the closure’s spatial and temporal limits is necessary to ensure spawning biomass or if current management is sufficient.

Keywords: recreational fisheries, migration, marine protected areas, reproduction, fishery management
Introduction

A diverse array of fishes aggregate to spawn, including epinephelids, carangids, labrids and sparids (Sadovy de Mitcheson and Colin 2012). Fish spawning aggregations (FSA) are usually predictable, occurring repeatedly at specific sites at the same time of year, during particular environmental cycles (e.g. lunar phases, water temperatures, diel cycles, tidal regimes etc.) and with fish using the same migratory pathways to join them (Zeller 1998; Wakefield 2010; Domeier 2012; Nanami et al. 2014). This predictability and associated increase in catchability has led, in many cases, to overexploitation of spawning aggregations via commercial, subsistence and/or recreational fishing (Sadovy de Mitcheson and Erisman 2012; Grüss et al. 2014; Sadovy de Mitcheson 2016).

Spatial and temporal closures to fishing are often implemented to protect FSAs. However, of 17 reviewed closures, less than half (43%) led to purported species benefits, such as increases in abundance or body size, and only 17% indicated specific fisheries benefits, e.g. increased yield or catch per unit effort (Grüss et al. 2014). Expected benefits of fishing closures to FSAs or the broader stocks are influenced by the (1) often transient nature of aggregating fish vs the fixed spatio-temporal constraints of closures to fishing, potentially leaving adults exposed to exploitation when not aggregating, (2) variation in whether all or only part of the adult population aggregates to spawn and (3) limited understanding of the complex patterns of behaviour and movement of species that aggregate-spawn, such as predictability of migration pathways, spawning site philopatry and habitat use (Zeller 1998; Erisman et al. 2017). This information is critical if implemented closed areas are expected to contribute to resource management (Heupel et al. 2006).

The sparid *Chrysophrys auratus* (Forster 1801) supports large commercial and recreational fisheries in Australia and New Zealand, including the targeting of its spawning aggregations (e.g. Parsons et al. 2009; Hamer et al. 2011; Sadovy de Mitcheson and Colin...
2012). On the west coast of Australia, this functional gonochorist only aggregates to spawn in
two regions almost 1 000 km apart at ~26 and 32°S (Wakefield 2010; Jackson and Moran
2012; Fig. 1). Peak spawning occurs when water temperatures are within a narrow range
(~19-21°C) and thus at different times of the year in the latitudinally separate regions. At
32°S on the lower west coast, this usually occurs during austral spring (around November),
although spawning can extend from August to January (Wakefield 2010; Wakefield et al.
2015). The restricted environmental parameters for peak spawning by *C. auratus* would
contribute to its high interannual recruitment variation, which may include spawning
omission in some years and latitudinal variation in recruit abundance (Francis 1993; Fowler
and Jennings 2003; Sim-Smith et al. 2012; Wakefield et al. 2015; 2017).

On the lower west coast of Australia, *C. auratus* can reach over 1 300 mm total length
and 40 y, and matures at ~6 y and ~600 mm, making it inherently vulnerable to fishing
(Randall et al. 1997; Norriss and Crisafulli 2010; Wakefield et al. 2015). These large fish
aggregate to spawn in three adjacent marine embayments at ~32°S, that are close to the major
population centre of this region. Here, they are exposed to substantial anthropogenic
activities, including industry and ports, naval and trade vessels, recreational boating and
fishing (Wakefield 2010; Wakefield et al. 2013a). The aggregations are easily accessible and
historically they were fished both commercially and recreationally until an annual six-week
closure (15 Sept-31 Oct) to fishing for *C. auratus* in two of the embayments (Cockburn
Sound and Warnbro Sound) was introduced in 2000 (Fig. 1). This was extended to four
months (1 Oct-31 Jan) by 2005 to better protect fish during their spawning period
(Wakefield, 2010). As demersal species such as *C. auratus* are a major target of commercial
and recreational fisheries along the broader west coast and they had experienced overfishing,
significant changes to management were made between late 2007 and early 2010 to recover
stocks (Wise et al. 2007). Commercial fishing for these species became limited to permitted
vessels in late 2007, which were prohibited from fishing in the Metropolitan Area of this coast (31-33°S, Fig. 1). Recreational fishing from private- and charter-boats is allowed in the Metropolitan Area under input and output controls introduced at the end of 2009. These included a two-month (15 Oct - 15 Dec) fishing closure for demersal species in the West Coast Bioregion (WCB; Fig. 1), boat-fishing licences and small daily bag limits (two demersal fish per person). The minimum length for retention of *C. auratus* was also increased to 500 mm total length for both sectors in the Metropolitan and South-west Areas of the WCB (see Fig. 1).

Adult *C. auratus* tagged in the embayments in the spawning periods from 2003 to 2016 during this and previous studies disperse after spawning, with ~79% of fish recaptured < 20 km from the embayments (Fig. 2a; Wakefield et al. 2011). About 91% of recaptures have occurred within 4 y of tagging and 72% during the same or subsequent spawning seasons, i.e. Aug-Jan (Fig. 2b; Wakefield et al. 2011; 2015). A small number of *C. auratus* have been recaptured ~100-700 km from the embayments (Fig. 2a). However, otolith microchemistry of *C. auratus* in this region indicated that adults typically do not move distances greater than the scale of the large management areas along this coast, e.g. the Metropolitan Area, which encompasses the embayments (Fairclough et al. 2013). Such patterns are broadly consistent with movement variation described for this species in small-to large-scale studies across Australia and New Zealand (e.g. Moran et al. 2003; Parsons et al. 2014; Harasti et al. 2015; Fowler et al. 2017). The recapture of fish in the lower west coast embayments indicates that, if they did leave following the spawning period in which they were tagged, they also returned. However, this does not demonstrate whether they return to spawn in multiple or consecutive years, given the nature of mark-recapture methods. While spawning also occurs in surrounding marine waters and along the extensive coast beyond the Metropolitan Area (Lenanton 1974; Lenanton et al. 2009; Wakefield et al. 2011), there may
be selective advantages in returning, as oceanography in the embayment facilitates the
retention of eggs and larvae, ensuring recruits remain in relatively more productive waters
during early life (Lenanton 1974; Wakefield 2010; Wakefield et al. 2011).

Biological studies have contributed critical information to the spatial management of
*C. auratus* across this extensive coastline. Knowledge of the reproductive behaviour and peak
spawning times in the embayments specifically, informed the introduction of the spatio-
temporal fishing closure to protect aggregations (Wakefield 2010; Wakefield et al. 2015).

However, despite this knowledge and the comprehensive management of this species,
locations and timing of migrations in relation to the closure on the lower west coast have not
been assessed and thus neither has the exposure of migrating *C. auratus* to fishing.

Acoustic telemetry is frequently used to identify fine-scale movement patterns, that
mark-recapture data does not. It has been used to investigate the potential effectiveness of
spatial closures for protecting species or stocks (e.g. Meyer et al. 2010; Parsons et al. 2010;
Abecasis et al. 2009; 2015), but rarely in fisheries management (Sadovy de Mitcheson et al.
2008; Donaldson et al. 2014; Crossin et al. 2017). Over three years, we examined the spatial
and temporal patterns of occurrence of adult *C. auratus* in relation to the three embayments
on the lower west coast of Australia where it aggregates to spawn. Data were used to infer
migration patterns to and from the main embayment of Cockburn Sound. Detection data from
an acoustic receiver array, which included receivers provided by the Canada Foundation for
Innovation-funded international Ocean Tracking Network, were used to (1) determine the
entrance/exit pathways used by individuals to migrate, (2) identify the timing of immigration
and emigration and (3) evaluate the hypothesis that individuals exhibit spawning site
philopatry by returning to Cockburn Sound in consecutive years. These lines of evidence
were then used to investigate the potential for exploitation of migrating *C. auratus* given
current spatial management arrangements, broader stock management measures and available
data on fishing in the vicinity of the embayments.

Materials and methods

Sampling regime

*Chrysophrys auratus* were caught by line fishing during the spawning periods in 2009
(n = 30) and 2010 (n = 10) on the lower west coast of Australia, either between Garden and
Carnac Island (Site A), or at locations within Cockburn Sound (Sites B and C; Supplementary
Table 1; Fig. 1). Each fish was placed in a circular 250 L plastic tank with aerated seawater
and anaesthetised using clove oil (0.27 ml L$^{-1}$ seawater) until stage II anaesthesia, i.e. ~60 s
(Munday and Wilson 1997). Fork length was then measured to the nearest 1 mm and sex
determined by cannulation or during surgery if possible. Each fish was laid inverted in a v-
shaped foam support covered in wet plastic and its gills irrigated with fresh seawater. A
Vemco© acoustic transmitter (V16-4H, V13-1L, V13-1H) was inserted into the body cavity
via a ~3 cm incision in the abdominal wall, ~2 cm anterior of the cloaca and 1 cm lateral of
the ventral mid-line. The incision was closed using absorbable sutures (Ethicon Vicryl CP-1
with 36 mm, $\frac{1}{2}$ circle reverse cutting needle) and the fish injected with Bivatop antibiotic
(200 mg mL$^{-1}$ tetracycline) at 0.1 ml kg$^{-1}$ of body weight, estimated using the fork length-total
weight relationship of Wakefield et al. (2015) (Supplementary Table 1). Two 13 cm dart tags
(PDS: Hallprint ©) were inserted into the dorsal musculature of each fish for potential
recapture identification. Fish recovered from anaesthesia in a 500 L tank of aerated sea water
until they oriented and swam independently, which took 2-11.5 min (mode = 3 min). Fish
were then immediately released. The time between capture and release ranged from ~7.5-
17 min (mode = 9 min; based on data recorded for 21 fish). In Western Australia, the Animal
Welfare Act 2002 does not require the Department of Primary Industries and Regional
Development to obtain a permit to use animals (fish) for scientific purposes unless the species are outside the provisions of the governing legislation (i.e. Fish Resources Management Act 1994 and Fish Resources Management Regulations 1995). However, all sampling was undertaken in strict adherence to the Department’s Policy for the handling, use and care of marine fauna for research purposes. In addition, surgery was conducted following methods of previous ethically approved work (Fairclough et al. 2011) and with input from the Department’s Animal Health staff and is consistent with the guidelines of the Committee for the Update of the Guide for the Care and Use of Laboratory Animals (National Research Council 2011).

No significant difference (Kolmogorov-Smirnov two-sample test, $D_a = 0.035; \ df = 1; p > 0.05$) was identified between the length frequency distributions of the *C. auratus* tagged for telemetry and a larger sample of *C. auratus* ($n = 549$) captured from the same spawning aggregations during 2009 and 2010 (Fig. 3). Thus, the sample of *C. auratus* used for telemetry was considered representative of the broader population that aggregated to spawn in Cockburn Sound during the study period.

**Receiver array**

Vemco© receivers were deployed across five potential pathways to Cockburn Sound to produce double-gates that could detect immigration and emigration of *C. auratus* (Fig. 1). Cockburn Sound is bounded at its northern end by a shallow bank, while at the southern end, a narrow, shallow passage between Garden Island and the mainland delineates the embayment from the open ocean. The five pathways each comprised two lines of receivers:

1. (1) Rottnest Island to Fremantle and Garden Island to Woodman Point,
2. (2) Rottnest Island to Straggler Rocks and Garden Island to Woodman Point
3. (3) Straggler Rocks to Carnac Island and Garden Island to Woodman Point
(4) Carnac Island to Garden Island and Garden Island to Woodman Point, and

(5) the southern end of Garden Island and the mainland.

The array comprised 47 VR2W receivers (the ‘aggregation array’), 53 VR2Ws in the Canada Foundation for Innovation-funded international Ocean Tracking Network’s Perth line (OTN; [http://oceantrackingnetwork.org](http://oceantrackingnetwork.org); Cooke et al., 2011) and 19 VR2Ws and 20 VR4Gs that form the Metropolitan component of the Department's Shark Monitoring Network (SMN; McAuley et al. 2016). For analyses, the gate represented by Site A comprised the western line of seven receivers between Garden and Carnac islands and the nine most western receivers between Garden Island and Woodman Point (Fig. 1). As part of the ‘aggregation array’, a VR2W was deployed at site B and C in Cockburn Sound and at three locations in Warnbro Sound, where *C. auratus* also aggregate to spawn. A temporary array of 19 receivers was deployed in Cockburn Sound from Dec 2009–Feb 2010 and Aug 2011–Mar 2012 to increase the potential for detection of *C. auratus*. The SMN also comprised cross-shelf lines of VR2Ws deployed in Apr/May 2012 off the south-west (48 VR2Ws) and western south coasts of Australia (two lines, 44 and 33 VR2Ws; Fig. 1). Receivers in the SMN and OTN arrays were deployed at 800 m intervals (McAuley et al. 2016).

Each VR2W in the aggregation array was attached to a stainless-steel pole mounted vertically in a concrete-filled car tyre. VR2Ws were deployed ~500 m apart in water depths of 4–17 m, at locations not obstructed by reef structure. Distances between receivers were determined from (1) knowledge of an expected range of 525 m for V16-4Hs (158 dB re 1 µPa @ 1 m) in wind conditions of 28–34 knots ([https://vemco.com/range-calculator/](https://vemco.com/range-calculator/)) and (2) range testing of a V16–4H (fixed 120 s delay) in the study area, where detections decreased by 50 and 95% of the theoretical maximum number per day by 531 and 717 m, respectively (How and deLestang 2012). Receivers were retrieved from the water annually to remove fouling, download data via Vemco VUE (version 1.6.5) and install new batteries.
Analysis of detection data

Detection data from all receivers in all the arrays were kept within a central data management system. This contained transmitter ID, date and time, spatial coordinates of receiver (decimal degrees), Receiver Station ID and depth of Receiver Station associated with transmitters detected from this study and tagged sharks from other studies (McAuley et al. 2016; Braccini et al. 2017). The False Detection Analyser in Vemco VUE v2.30 was used to identify false transmitter detections; i.e. Type A (invalid transmitter codes, which can be produced as a result of environmental sounds or transmitter code collisions) and Type B (false detections of valid transmitters due to detections occurring on a single receiver at shorter time intervals than the programmed ping rate) (Heupel et al. 2006; Simpfendorfer et al. 2015). Approximately 0.01% of a total 3.5 million detections were Type A false detections, with the vast majority occurring at site B. These would have been influenced by the six V16 transmitters which produced almost continuous detections at that site and may have been deceased fish. These were removed from analyses (see later in Methods). While the cause of false detections could not be ascribed to transmitters used in this study, due to transmitters also having been deployed for other studies simultaneously, they represented a very low percentage of total detections and would have had little effect on the outcomes of the analyses. No Type B false transmitter detections were identified. A further 195 detections from one fish were removed due to a receiver station code transcription error.

Data were analysed using R (R Core Team, 2017). Six *C. auratus* with V16 transmitters contributed ~2 million detections to the total 3.5 million during the study and were all recorded at site B (Fig. 1). As these detections were essentially continuous, it was not possible to distinguish whether these fish had become resident or were deceased and still within proximity of the receiver. Daily variations in detection rates may have been caused by
environmental or anthropogenic noise interference, rather than movement towards and away from the Site B receiver or a combination of all these factors. These data were omitted from analyses. One fish (#60358) was predated on by a shark at the time of release (pers. obs.) and thus its detections were removed from analyses.

Detections from the remaining 33 *C. auratus*, with 23 V16 and 10 V13 transmitters were used to determine the locations of entry to or exit from Cockburn Sound, while only the V16 transmitters were used to investigate migration timing and philopatry after 2009/10. These transmitters were programmed to last for ~ 1000 d, with short and long delay periods to coincide with spawning months and non-spawning months, respectively. The V13 transmitters were surplus from other studies and were beyond their recommended shelf life. Thus, they were potentially less reliable for analyses of timing of migrations. The daily presence/absence of each *C. auratus* within the entire array (aggregation array, OTN and SMN) was determined from the day it was released until either its last detection within the array (if this occurred before the end of the transmitter’s expected life) or the estimated end of the transmitter’s life (see Supplementary Table 1). The sequence of detections of each fish in double gate arrays at each entrance/exit and/or at receivers inside Cockburn Sound were used to evaluate directionality of movement.

As detections of *C. auratus* among the five potential gates occurred almost exclusively at the gate between Garden and Carnac islands, i.e. Site A (see Results), these data were used to evaluate whether there was evidence of immigration and emigration via a bimodal pattern of occurrence at Site A and whether it was consistent among years. This was predicted to occur based on the expectation that *C. auratus* move into and out of Cockburn Sound prior to and after the spawning period, respectively. These analyses were also used to relate this movement to the timing of the spatio-temporal closure, commencing on 1 Oct each year. The number of unique *C. auratus* detected from 1 Aug to 28 Feb in 2010/11 and
2011/12 in each discrete week (7 days) prior to and after 1 Oct in each year was expressed as a proportion of the total possible number of transmitters that could be detected in each year (i.e. 20 fish, which did not include the three fish which became resident at Site A or inside Cockburn Sound). The data were assumed to be normally distributed around a mean week of immigration and emigration. Single, bimodal and tri-modal finite mixture distribution models were fitted to the data for each year according to the function $F(x) = \sum_{i=1}^{n} w_i P_i(x)$, where $P_i(x)$ is the probability density function for each distribution (with mean $\bar{x}$ and standard deviation $\sigma$) and $w_i$ is the weight of each distribution, such that $\sum w_i = 1$. Model parameter estimates were derived using a maximum likelihood approach. Akaike Information Criterion (AIC) values were calculated to determine which of the models provided the best fit (lowest AIC), where $AIC = -2LL + 2K$ and $K$ is the number of parameters in the regression equation (including the estimate of the residual variance). Models were compared after adjusting for sample size, as the ratio of $n/K$ was less than 40 ($n$ is the sum of the number of transmitters observed per week from 1 Aug to 28 Feb), as follows: $AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$ (Burnham and Anderson 2002). Note that the assumption of the presence/absence data being gamma distributed was also evaluated using single, bi- and tri-modal mixture models. However, the shapes of the fitted distributions and their log likelihoods were similar to those of the normal distributions in each case in each year. The bimodal model again produced the lowest $AIC_c$ values. Thus, the normal distribution fits were considered appropriate. Daily sea surface water temperature (SST) data (multi-scale ultra-high resolution SST analysis fv04.1, 1 km resolution) were obtained for an area bounded by 32.1-32.2 °S and 115.6-115.7 °E from 1 Aug to 28 Feb in 2010/11 and 2011/12 from https://coastwatch.pfeg.noaa.gov/erddap/griddap (downloaded 6 April 2018). Moon fraction (percentage full) data were obtained for the same period from http://aa.usno.navy.mil/data/docs/MoonFraction.php (downloaded 6 April 2018). Mean weekly SST and moon fraction were then calculated, as per detection data.
Fishery and biological data

Fishery and biological data were obtained from time periods as close as possible to that of the telemetry study. These data were used to provide general patterns of fishing for *C. auratus* and of its reproductive biology. Available retained catch data for *C. auratus* from the commercial and recreational sectors were used to provide an indication of the typical spatial distribution of catches per year by the two sectors across the four management areas of the west coast. These include the Kalbarri (from 26°30′–28°S), Mid-west (28–31°S), Metropolitan (from 31–33°S) and South-west areas (from 33°S on the west coast to 115°30′E on the south coast; Fig. 1). Commercial fishing for *C. auratus* in the Metropolitan Area has been prohibited since 2008, other than by a small line fishery which occasionally catches *C. auratus* (Fairclough et al. 2014a). Catch data from compulsory logbooks of commercial line fishers between 2008 and 2016 were used to calculate the average annual commercial catch from each area. The recreational sector comprises both charter- and private-boat fishers. Catch data from charter-boat fishing between 2008 and 2016 were obtained from compulsory Tour Operator Returns and used to calculate their average annual catch for each area. As catches from private-boat based recreational fishing are not surveyed annually, estimated annual catches from each area were derived from a recent one year survey of recreational fishers during 2013/14, which integrated phone-diary surveys and boat-ramp validation surveys (Ryan et al. 2015). These estimates were combined with the average charter catches by area to provide an estimate of the typical average annual catch of the recreational sector in each area. The average annual catches of *C. auratus* in each area by the commercial and recreational sectors were then used to calculate the percentage of the total catch taken by each sector in each area.
Charter- and private-boat data were further examined to infer any changes in fishing activity (targeting) associated with the presence of migrating or aggregating *C. auratus*, prior to, during and after the spawning period. Reported catches by charter-boats in each 10×10 nm block in the Metropolitan Area (encompassing the area of the study) in each month in 2015/16 were plotted to identify the spatio-temporal distribution of their catch. These data are not available for private vessels. Thus, to provide information on private vessel activity in the area of the study, the estimated number of powered-vessel launches was determined for each hour of the day in each month from March 2011 to February 2012, calculated from footage obtained from a remote camera installed at Woodman Point, typically the Metropolitan Area’s most-used boat ramp (Fig. 1; Ryan et al. 2013; 2015). Although not all vessels launched are used in fishing activities, the number of launches is positively correlated with recreational fishing effort and thus provides an index of fishing effort (Steffe et al. 2017).

Data on the frequency of occurrence of *C. auratus* in the Metropolitan Area, including Cockburn Sound, that contained either stage III (i.e. developed or pre-spawning) or stage IV (i.e. ripe or spawning) ovaries between 2002 and 2006 were obtained with permission from Wakefield et al. (2015). The percentage frequency of these two stages in each month of the year was used to compare the timing of the spawning period to the timing of detections within the array and the annual closure to fishing in the embayments. Although this work was conducted prior to the telemetry study, other studies of *C. auratus* in Cockburn Sound that have focused on aspects of its reproductive biology (e.g. egg production) provide evidence of consistent interannual timing of the spawning period (cf. Wakefield 2010; Dias et al. 2016; Partridge et al. 2017).
Results

Over one million valid detections of *C. auratus* with transmitters were recorded throughout the study by the aggregation, OTN and SMN arrays combined. The total number of detections of individual transmitters ranged from 113 to 265,742, while V16 transmitters were detected on up to 675 d (\(\bar{x} = 148.5\) d; Supplementary Table 1) over the three year study. The majority of *C. auratus* detections (~83%) occurred between September and January, with > 99% of those recorded from 29 of the 33 valid transmitters at Site A (the line of seven receivers between Garden and Carnac islands and the nine most western receivers between Garden Island and Woodman Point) and sites B and C inside Cockburn Sound (Figs 1, 4, 5). Relatively few *C. auratus* were detected in the other pathways to Cockburn Sound, i.e. eastern receivers between Garden Island and Woodman Point (< 1% of detections, 10 fish), Rottnest Island to Fremantle (< 1%, 13 fish), Rottnest Island to Straggler Rocks and Carnac Island (< 1%, 8 fish) and the southern end of Cockburn Sound (< 1%, 4 fish) (Fig. 4).

Timing of detections in relation to the fishing closure and environmental parameters

Detections of V13 and V16 transmitters provided strong circumstantial evidence of sequential movement to and/or from Cockburn Sound. After fish were tagged in 2009, 25 of the 29 V16 and V13 transmitters detected at sites A (Garden Island to Carnac Island), B or C (inside Cockburn Sound) between October and December 2009 were subsequently detected at Site A before the end of the closure to fishing on 31 Jan 2010 (Fig. 5). Twenty three of those 25 ceased to be detected at Site A by 31 Jan. One remained at Site A for a further 1.5 y and then was no longer detected (#60352), while another (#1367) was detected again at Site A in early February 2010. Fourteen fish were subsequently detected outside the embayment on SMN or OTN receivers between Garden and Rottnest islands, or briefly east of Site A, towards Woodman Point. Four of the 29 fish continued to be detected at Site B in the
embayment where they were tagged. However, three of those (#60361, 60639, 60371) ceased
to be detected by 31 January, while one (#51857) was detected until early February 2010 at
Site B and then once in April 2010 outside the embayment, immediately north of Carnac
Island (Fig. 5).

Of a possible 23 fish with valid V16s, six of the 17 fish detected during the 2010/11
closure and 9 of the 15 fish detected during the 2011/12 closure were first detected prior to
the closure commencing on Oct 1 (Fig. 5). This occurred 32-36 d before the closure in those
years, respectively, either beyond the Site A gate on SMN or OTN receivers, at Site A or at
Site B. In contrast, the last detections of almost all fish at either Site A or B in the 2010/11
and 2011/12 spawning seasons were recorded before the end of the closure to fishing on 31
Jan. During the 2010/11 spawning period, six of 19 fish with V16s were recorded
consecutively at Site A, followed by Site B or C within Cockburn Sound and then five were
later recorded at Site A (Fig. 5). Seven fish were only detected at Site A, two of which
demonstrated evidence of residency and one was only detected late in November, thus later in
the spawning period. A hiatus in detections occurred at Site A with four of the seven fish,
during which time they were not detected elsewhere. However, three were last detected on
the eastern (or inside) line of receivers leading in to Cockburn Sound. While three fish were
not detected that year, the remaining three were detected at only Site A early in the spawning
season or only at Site B intermittently during the spawning season. Of the four fish tagged at
Site B in the 2010/11 spawning season with valid V16s, each was detected for a period at Site
B and three were subsequently detected at Site A before the end of the closure.

Of 23 valid V16s, detections at Site A, followed by Site B and then Site A were
recorded for two fish in 2011/12. Another 10 fish were detected at Site A, but not inside
Cockburn Sound. Four of those exhibited a hiatus in detections, preceded by detections on the
eastern (or inside) line of receivers at Site A. Three fish were detected intermittently only
inside Cockburn Sound, while one was only recorded outside Cockburn Sound, detections of another two indicated residency at Site A or B and five fish were not detected.

Across all years of the study, the relatively small number of detections (n = 5576) of 22 transmitters on receivers other than at Site A, B or C between September and January occurred over short periods and for the majority of these fish (n = 17) indicated sequential movement to and from Site A. For example, two individuals (#60366 and 60370) were detected on OTN and SMN receivers near Fremantle in Oct 2010 over one and five consecutive days, respectively (808 detections not visible on Fig. 4). They were preceded by detections at Site A 2.2 and 1.25 d before, respectively, and followed by detections at Site A 0.4 d later and Site B 0.9 d after that. Fish #60370 was then detected at Site B for 44 d and at Site A 0.25 d later. Two C. auratus (#60364, 60368) were detected briefly (12 detections over 33 min; 6 detections over 17 min) on the two western-most receivers of the southern entrance of Cockburn Sound in Aug and Oct 2010 and subsequently on the western receivers at Site A 15 h and 3.8 h later, respectively. Another two individuals were detected in Warnbro Sound for short periods (#60360 for 2 d in Nov 2010 and 5 d in Oct 2011; #60368 for 13 d in Oct 2010) and subsequently at Site A within ~1 d.

The number of fish with V16 transmitters detected at Site A in each week between 1 Aug and 28 Feb in both 2010/11 and 2011/12 had a bimodal frequency pattern. AIC_c values indicated that bimodal mixture distributions produced the best fit to these data in each year, in comparison to both single mode and tri-modal models (Table 1). In both the 2010/11 and 2011/12 spawning seasons, the number of fish detected at Site A began to increase prior to the commencement of the closure on 1 October, while mean water temperatures were < 19 °C (Fig. 6). The first of the means of the bimodal distributions occurred at ~ 1.0 and 0.6 weeks after the commencement of the closure in 2010/11 and 2011/12, respectively, when water temperatures were ~19 °C (Table 2, Fig. 6). Fewer fish were detected during subsequent
weeks, with the lowest frequencies recorded while water temperatures were < 21 ºC and at
the time of the new moon in November in 2010 and between the approximate times of the
new moons in October and November in 2011 (Fig. 6). This occurred when the percentage of
female *C. auratus* in Cockburn Sound with ovaries in pre-spawning/spawning condition is
typically increasing to or is at its maximum (Fig. 6; cf. Figs 4, 8, 9). The second mode
occurred at 9.6 and 8.0 weeks after the closure commenced, when water temperatures had
reached 21 ºC in both years (Table 2; Fig. 6). Frequencies of occurrence then declined as
water temperatures increased above 21 ºC, which occurred before the end of the fishing
closure on 31 Jan in both years and as the percentage of females with ovaries in pre-
spawning/spawning condition declined (Fig. 6, cf. Figs 4, 7, 9). The standard deviation of the
mean number of fish detected per week indicated relatively consistent variation around the
two means in 2010/11, but the second mean in 2011/12 exhibited less variation than the first
and less than both means in 2010/11 (Table 2; Fig. 6).

**Spawning aggregation philopatry**

The majority (*n* = 21) of the 23 *C. auratus* with V16 transmitters were detected either
at Site A, B or C in at least one spawning season subsequent to being tagged. Seven fish were
detected in only one spawning season following tagging with two of those only detected
again two years after being tagged. Ten and four fish were respectively detected in two and
three consecutive seasons after being tagged. However, two of the latter four fish appeared to
remain at site A or site B for extended periods including the non-spawning period. Although
unexpected, two of the ten fish with V13 transmitters were also detected in one or two
subsequent spawning seasons (Fig. 5). After detection at sites A and B in two consecutive
spawning seasons after being tagged, one fish (#60360) was detected once in March 2012 on
the SMN array #1, ~240 km south of the embayments, while another (#60362) was captured and retained by a recreational angler ~135 km north of the embayments.

**Fishing Effort**

The majority of the average annual retained catch of *C. auratus* in the WCB is taken by the commercial fishery in the Kalbarri (26°30′-28°S) and Mid-west areas (28-31°S), i.e. ~74% (Fig. 7). The recreational sector lands ~25% of the average annual catch in the WCB, of which, ~14% is taken in the Metropolitan Area (31-33°S; Fig. 7). Average annual retained charter fishing catches comprise 32% of the recreational sector catch in the WCB and the largest component of that (16%) is from the Metropolitan Area (not shown in Fig. 7).

In the Metropolitan Area, the largest monthly catches (102-200 fish per 10×10 nm block) from charter boat recreational fishing typically occurred west, north or north-west of Rottnest and/or Garden islands (Fig. 8). In July to October, leading up to the peak of the spawning season, the closure to fishing for *C. auratus* in the embayments (1 Oct-31 Jan) and the closure to fishing for all demersal species, including *C. auratus*, across the WCB (15 Oct-15 Dec), catches were reported only in blocks north of Garden Island (~36.15°S; Fig. 8). The largest of these catches per block were concentrated mostly between Rottnest and Garden Islands and particularly the block encompassing Site A. Between December and March, i.e. towards the end of, and following the spawning season, the largest total catches per block were reported from the same area between Rottnest and Garden islands, but catches were also widely dispersed across the Metropolitan Area, including southwards from Garden Island.

From April to June, charter catches were typically low and dispersed northwards from Garden Island.

At Woodman Point, the majority of vessel launches in each month occurred in the morning from ~06:00-12:00, followed by relatively fewer launches for the rest of the day and
night (Fig. 9). However, in August and September, just prior to the October commencement of the fishing closure, a prominent second mode of launches was detected in the late afternoon/dusk. During these two months, ~30 and 44% of adult female \textit{C. auratus} in the Metropolitan Area contained ovaries which were in pre-spawning or spawning condition (Fig. 9). This is in contrast to the 68% of adult females with ovaries in pre-spawning or spawning condition in October and > 92% in November and December, when spawning is typically at its maximum in that area. These months also exhibited a unimodal frequency of boat launches in the morning, when fishing for \textit{C. auratus} is prohibited. By January, adult female \textit{C. auratus} with ovaries in pre-spawning or spawning condition have declined below 50%, and after January when fishing is allowed, little spawning activity occurs (Fig. 9).

**Discussion**

This study used acoustic telemetry to determine the migration patterns of \textit{C. auratus} to and from an embayment on the lower west coast of Australia where it aggregates to spawn and is protected by a spatio-temporal fishing closure. Detections of \textit{C. auratus} indicated predictable and repeated movement behaviours consistent with the relationship between reproduction and environmental parameters in this species. Individuals (1) migrated via only one of several pathways into the main embayment of Cockburn Sound where spawning occurs, (2) often occurred in that pathway before the fishing closure began and spent varying periods of time there, but most left before the closure ceased, (3) were detected in the pathway and/or aggregation locations in the embayment in more than one year, confirming spawning site philopatry, but (4) may not always return in consecutive years. The spatio-temporal closure offers limited protection to migrating and pre-spawning fish, as individuals begin arriving at the main pathway before the closure commences and are fished there and over adjacent reef systems at that time. This is likely to impact spawning aggregation.
biomass. Assessment and monitoring of mortality or spawning biomass would help to identify whether current management is sufficient to ensure the sustainability of the aggregations and their contribution to the broader stock.

**Biological relevance of *Chrysophrys auratus* movements**

Recurrent detections of *C. auratus* in only one of the several pathways to the main embayment in which they aggregate-spawn implies that this pathway provides navigational cues for migration. The pathway lies just to the east of two north-south oriented reef systems (the Garden Island ridge on the western side of the island and Five Fathom Bank further to the west), which both extend southwards from the south-eastern end of Rottnest Island, past Garden Island and, in the case of Five Fathom Bank, beyond 33°S (Fig. 1). Migrating fish may use these to navigate to and from the pathway to Cockburn Sound, which is supported by the recapture of tagged *C. auratus* along Five Fathom Bank and is consistent with the locations of charter catches of *C. auratus*. These and other reef lines in deeper water (~80 and 110 m) along the west coast may provide important pathways that some *C. auratus* use to disperse substantial distances from Cockburn Sound as recorded during this and previous studies (Wakefield et al. 2011). Reef lines and shelf margins or ridges comprise obvious bathymetric characteristics which are commonly-used by demersal fishes, such as epinephelids, to migrate to aggregation sites. This usage may be a learned behaviour, particularly in the case of young maturing fish (Domeier and Colin 1997; Starr et al. 2007; Colin 2012; Nemeth 2012; Sadovy de Mitcheson 2016). In southern Australia, *C. auratus* also demonstrates systematic habitat/location use patterns, dispersing across areas of > 100 km² from a location, but revisiting that location at the same time in different years (Fowler et al. 2017). The pathway in to Cockburn Sound used by *C. auratus* may also provide resources that others do not, such as habitat that offers protection from predation or food. As some...
C. auratus may migrate substantial distances, continued feeding may be necessary to provide energy for gonadal development and spawning, as in the carnivorous Epinephelus guttatus and herbivorous Chlorurus sordidus (Sancho et al. 2000; Nemeth 2012; Kawabata et al. 2015).

Acoustic telemetry has demonstrated that the timing of entry to and departure from Cockburn Sound is consistent with the strong link between the reproductive periodicity of spawning aggregations of C. auratus in the embayment and annual, lunar, diel and oceanographic cycles (cf. Scott et al. 1993; Wakefield 2010; Saunders et al. 2012; Wakefield et al. 2015). A bimodal frequency of occurrence of C. auratus was identified in the main pathway to Cockburn Sound in both 2010/11 and 2011/12, with the first and second modes in each year corresponding with the time when water temperatures were ~19 and 21°C, respectively. Spawning peaks in these waters within that narrow temperature range, which typically occurs in November (late austral spring), while gonadal atresia occurs when water temperatures exceed 21°C, usually in December/January (summer) (Wakefield 2010; Wakefield et al. 2015). Thus, the two modes presumably reflect periods of accumulation in the pathway, as individuals migrate to and from the aggregations and this migration is linked with water temperature. The trough between the two modes would represent the time during which most individuals are within Cockburn Sound, consistent with the detections of tagged fish at sites in the embayment. This period coincided with one or more new and full moons in 2010/11 and 2011/12, during which greater spawning activity typically occurs, particularly on the new moon that coincides with water temperatures of 19-21°C (Wakefield 2010). The difference in the number of new moons experienced in the time during which water temperatures rise from 19 to 21°C may thus influence the extent of spawning activity in any one year.
As there is a strong relationship between water temperatures and gonadal maturation, migration and/or formation of spawning aggregations of *C. auratus*, predicted ocean temperature increases (Pearce et al. 2016) may influence the timing or location of those behaviours. This would alter the efficacy of the associated spatio-temporal fishing closure (Sheaves 2006; Jackson et al. 2015; Wakefield et al. 2015). Furthermore, marine ‘heatwaves’ have increased in duration and frequency in the last century (Lenanton et al. 2017; Oliver et al. 2018), which may have rapid and unpredictable effects on *C. auratus* spawning success in the embayments. Individuals may no longer enter the embayment if water temperatures exceed the preferred range for successful spawning. Such phenological variations in relation to water temperature are common in marine organisms in shallow and deep waters across tropical and temperate regions, including among cephalopods (e.g. *Loligo forbesi*) and teleosts (*Dascyllus albisella, Platichthys flesus, Clupea pallasi, Gadus morhua, Hyporthodus octofasciatus*) (Lawson and Rose 2000; Sims et al. 2001; Asoh and Yoshikawa 2002; Sims et al. 2004; Wakefield et al. 2013b).

**Exploitation of migratory and aggregatory fish**

The predictability of spawning aggregations is the key reason they are susceptible to over-exploitation and consequent negative impacts on abundance and/or biology (e.g. Coleman et al. 1996; Sadovy and Cheung 2003; Erisman et al. 2012; Sadovy de Mitcheson and Erisman 2012). Fishing has the potential to extirpate aggregations and negate any selective advantage conferred by such behaviour and has often led to the need for significant management intervention. For example, while relatively few of the ~150 sparids aggregate-spawn (Nemeth 2012), some that do in southern Africa (*Petris rupestris, Polysteganus undulosus* and *Chrysoblephus gibbiceps*) are now endangered or critically endangered due to exploitation. This has led to complete closures to fishing for those species (Mann et al. 2014a,
2014b; Sadovy de Mitcheson 2016). Commercial and recreational fishing of aggregations of demographically separate but genetically-related *C. auratus* stocks on the upper west coast of Australia also resulted in stock depletions (Jackson and Moran 2012; Gardner et al. 2017). However, restrictive management to limit catches via a range of measures, including temporal closures and harvest tags, has allowed recovery of some of those stocks over 15+ years (Jackson and Moran 2012; Jackson et al. 2016). Recent overfishing of the coastal *Arripis georgianus* in the same region would be influenced by the exploitation of spawning biomass both during its pre-spawning migration along 100s to 1 000s of km of the southern Australian coastline and during the spawning period (Fairclough et al. 2000; Smith et al. 2013). Similarly, impacts of recreational fishing of migrating *Albula vulpes* in Kiribati resulted in the need for a fishing closure during its spawning period (Sadovy de Mitcheson and Erisman 2012).

Exploitation of *C. auratus* on the lower west coast of Australia by the recreational sector occurs along the reef systems between Rottnest and Garden islands, adjacent to the fishing closure, and in the main migratory pathway between Garden and Carnac islands. An increase in evening launches of private vessels at Woodman Point, the most proximal boat ramp to the main pathway, in August and September just prior to the fishing closure, is consistent with anecdotal information that recreational fishers target *C. auratus* at that time. The combination of telemetry and reproductive data (Wakefield 2010; Wakefield et al. 2015) confirms that fishers would be catching both pre-spawning migratory fish and fish that have become periodically resident in the area. However, not all fish may be exposed to fishing each year. Telemetry data also demonstrated that while the majority of fish were detected in subsequent years after tagging, exhibiting philopatry, other fish may have returned but were not detected, or may return but not in consecutive years. As some fish can travel substantial distances (100s of km) from the embayments, they may never return, instead living and
reproducing elsewhere. Such long distance movements have been documented in several studies of *C. auratus* (e.g. Parsons et al. 2014; Harasti et al. 2015), but the reasons for them are not known. Whether such individuals would return and what proportion of fish undertake this type of movement remains unclear. Thus, philopatry rates may be underestimated. This is similarly not well understood for aggregations of *C. auratus* in Port Phillip Bay in southern Australia (Hamer et al. 2011). Fish that travel substantial distances along the west coast of Australia are exposed to different levels of fishing mortality, associated with the varying management regimes, including different size limits and commercial fishing. Despite restrictive management of the spawning aggregations and broader stocks of *C. auratus* along the west coast, migratory fish are not protected until they have crossed the boundary of the spatio-temporal closure, after it has commenced. Thus, if exploitation of migratory pre-spawning *C. auratus* in the pathway and over adjacent reef systems is high enough, it may influence migratory patterns and/or reduce spawning biomass.

**Social importance and monitoring of Chrysophrys auratus spawning aggregations**

While recreational fishers enjoy targeting the seasonally amassing *C. auratus* in waters adjacent to or within the embayments, many presumably understand that targeting aggregations would have negative consequences. This recognition can increase their willingness to contribute to ensuring suitable management is in place (e.g. Hamilton et al. 2012; Heyman and Granados-Dieseldorff 2012). For example, public outcry occurred when over 250 *C. auratus* died during an environmentally driven fish-kill in Cockburn Sound around the time of peak spawning in 2015 (Department of Fisheries 2016). With recreational sector support and crowd-sourced funding, hatchery-reared juvenile *C. auratus*, originally bred for scientific purposes (Partridge et al. 2017), were released into the embayments on the premise that stocks would benefit. Government subsequently committed additional funding
for further releases of hatchery-reared juveniles in 2017 and 2018. The otoliths of released
fish are marked with alizarin red via immersion, allowing them to be identified at a later stage
if collected via *C. auratus* stock assessment sampling regimes (see Fairclough et al. 2014b).
However, the probability of this is low and there were no plans to evaluate the release
program with respect to its purported benefits to stocks or recreational fishing. The releases
are promoted as a mechanism to ensure ongoing occurrence of *C. auratus* in Cockburn
Sound, but given juveniles leave this embayment by ~18 months of age, disperse widely
along the coast and may not return, as occurs elsewhere in Australia, such benefits may never
be realised (Lenanton 1974; Fowler et al. 2005; Hamer et al. 2011; Wakefield et al. 2011).
Furthermore, such enhancement was not required to recover stocks of *C. auratus* on the upper
west coast of Australia, where traditional management methods, such as closures to fishing,
were adopted, accepted and successful (Jackson and Moran 2012, Molony et al. 2003). Thus,
education on the biology of *C. auratus* and the realistic benefits of stock enhancement vs
traditional input/output management controls is needed.

There are currently no data to demonstrate any decline in abundance of aggregating
*C. auratus* on the lower west coast since the fishing closure was introduced, which was
supported strongly by the recreational sector. Furthermore, the extent and effect of
recreational fishing of migratory *C. auratus* have not been measured. Surveys of private boat-
based recreational fishers’ catch and effort are conducted at larger spatial scales and are more
relevant to the broader stock on the west coast (Ryan et al. 2017). These surveys have not
detected a significant change in the total retained catches of *C. auratus* by private recreational
fishers between 2010/11 and 2015/16, but estimated catches have been at levels around the
predicted maximum that would allow stocks of *C. auratus* on the west coast to recover (Ryan
et al. 2017). However, the stocks are yet to recover and continued management is needed
(Fairclough and Holtz 2017). In addition, the number of private boat-based recreational
fishing licences in the metropolitan region, which is adjacent to the embayments, has increased by ~20% from 2010/11 to 2015/16, i.e. from ~57 000 to 69 000. Also, the numbers of C. auratus released by recreational fishers is very high, i.e. ~78% of fish landed in the Metropolitan Area in 2015/16, where a majority of the retained recreational catch is taken (Ryan et al. 2017). If post-release mortality is high in C. auratus, caused by factors such as barotrauma, gut-hooking and on-board handling (e.g. Stewart 2008; Grixti et al. 2010), or there are sub-lethal effects, such as skipped spawning, recovery of stocks or increases in biomass of aggregations may be restricted or prevented.

The social importance of the C. auratus spawning aggregations and their likely importance to its broader stocks along the west coast of Australia warrants further investigation and potential direct monitoring. This could benefit both management and the social desire for the aggregations to be sustained. A variety of methods may be applicable, but may vary in their cost-effectiveness. Assessment of age-based fishing mortality rates requires the collection of large numbers of fish from the aggregations, which would have undesirable impacts on biomass and reproductive behaviour. Mark-recapture models could be used to estimate fishing mortality, whereby aggregating fish are tagged and released. Estimation of aggregation biomass may be a more direct approach. This possibly could be achieved via daily egg production methods (DEPM), which have been used for C. auratus elsewhere (e.g. Jackson et al. 2012). However, DEPMs require significant laboratory time, as C. auratus eggs must be identified and counted from plankton surveys (Wakefield, 2010). This is challenging due to their visual similarities to eggs of other species, but the use of recently tested molecular identification techniques (real-time PCR and in-situ hybridisation) may help (Dias et al. 2016; Oxley et al. 2016). Acoustic surveys of aggregations using multi- or single-beam technology have been tested on other demersal species in this region and are commonly used elsewhere to estimate biomass (Rose 2003; Gastauer et al. 2017). However,
the relatively shallow waters of Cockburn Sound (< ~20 m) would require modifications to the technique, given they are normally used in deeper water. In addition, a dynamic survey design would be required that allows for the potential interannual variation in the timing of peak spawning due to environmental change and thus the potential to bias annual relative spawning biomass estimates. Determining the cost-effectiveness of the various methods and comparing the information they could provide to management in terms of responsiveness to changes in status (e.g. biomass) of the *C. auratus* aggregations would inform a discussion on which method may be preferable for long-term monitoring.

This study has explored the relevance of a spatio-temporal closure to fishing for *C. auratus* migrating to and from spawning aggregation sites in embayments on the lower west coast of Australia. This species exhibits predictable migratory patterns to and from the main embayment and, as a result, such fish are exploited by the recreational sector outside the embayment. Individual variation in the timing of migration and interannual philopatry to the aggregations may reduce the risk of capture. In addition, the current temporal and spatial extent of the closure protects the aggregations specifically, which is widely accepted by fishers. In conjunction with the restrictive management of stocks at the broader west coast scale, overexploitation of the spawning aggregations of *C. auratus* in lower west coast embayments is likely to have been avoided, but ongoing monitoring is required to ensure this does not occur in the future as the recreational sector grows. In addition, the effect that targeting of migratory fish may have on reproductive success of spawning aggregations may limit the benefits offered by current management, by interruption of migrations and removal of spawning biomass. Thus expansion of the spatial limits of the closure, to include the reef systems adjacent to the embayments where *C. auratus* are fished, or extension of the closure
to include August and September, when fish are beginning to arrive at the main pathway to
the embayment, may be required.

The importance of *C. auratus* spawning aggregations to the broader population along
the west coast of Australia is assumed, with progeny expected to disperse widely prior to
maturing. However, it is unclear to what extent this is the case. Indeed, aggregations in
southern Australia have been demonstrated to produce >70% of the recruits to ~800 km of
coastline (Hamer et al. 2011). Thus, identifying such source-sink relationships is important
and could be explored using contemporary genetic or possibly otolith microchemistry
techniques (Hamer et al. 2011; Ovenden et al. 2015; diBattista et al. 2017). Furthermore, such
an understanding would help to identify whether it is critical to monitor the status (e.g.
spawning biomass) of the spawning aggregations directly from a sustainability perspective, or
whether monitoring and appropriate management of fishing mortality of the broader stocks of
the west coast is sufficient to ensure the ongoing reproductive function of the aggregations
and also satisfy social expectations.

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Figure captions

**Fig. 1.** Study location in the inshore Metropolitan Area (cross-hatched on inset) of the West Coast Bioregion (WCB) of Western Australia. Inset shows main fishery areas of Kalbarri (K), Mid-West (MW) and South-West (SW) and Shark Monitoring Network arrays outside the Metropolitan Area (1,2,3). Main map shows (i) acoustic receiver arrays comprising the aggregation array (○) around Cockburn (CS) and Warnbro (WS) sounds and Owen Anchorage (OA), the Ocean Tracking Network (▲) and the Shark Monitoring Network (VR2W ■ and VR4W □) in the Metropolitan Area, (ii) the area closed to fishing for *Chrysophrys auratus* from 1 Oct-31 Jan (diagonal hatching), (iii) the five pathways to/from Cockburn Sound (arrows). OTN Receivers (▲) west of Rottnest Island extend to ~115°13´E (not all shown). A, tagging location and double gate array between Garden Island (GI) and Carnac Island (CI); B and C are tagging locations within Cockburn Sound; F, Fremantle; RI, Rottnest Island; S, Straggler Rocks; WP, Woodman Point. Map produced in ArcGIS v10.3 (ESRI 2014).

**Fig. 2.** (a) Recapture frequency of *Chrysophrys auratus* at different distances from tagging locations within the embayments and (b) frequency of recaptures in each month inside (black) and outside (grey) the area annually closed to fishing. Mark-recapture data derived with permission from Wakefield et al. (2011) for 2003-2009 is combined with ongoing data from the Department of Primary Industries and Regional Development for 2009-2016.

**Fig. 3.** Length-frequency distributions of *Chrysophrys auratus* tagged with dart tags (grey) and acoustic tags (white) in Cockburn Sound during the spawning seasons in 2009 and 2010.
**Fig. 4.** Proportion of total detections per month (combined across years) of *Chrysophrys auratus* at each receiver in the aggregation array, Ocean Tracking Network and Shark Monitoring Network calculated as $\frac{n \text{ detections per month per receiver}}{N \text{ total detections}}$; $n_{fish} =$ number of fish detected per month; $\%_{III/IV} =$ percentage of female *C. auratus* in each month with ovaries in pre-spawning (III) and spawning (IV) condition (from Wakefield et al. 2015). Red shading indicates the spatial area closed to fishing for *Chrysophrys auratus* from 1 Oct-31 Jan. CI = Carnac Island, CS = Cockburn Sound, F = Fremantle, GI = Garden Island, OA = Owen Anchorage, RI = Rottnest Island, S = Straggler Rocks, WP = Woodman Point. Maps produced in ArcGIS v10.3 (ESRI 2014).

**Fig. 5.** Daily detections of 34 *Chrysophrys auratus* at site A (black), outside the embayments (blue) and sites B and C inside Cockburn Sound (red), between the day they were tagged (Oct 2009-Dec 2009 or Sept 2010) and the day they were last detected. Expected end of each transmitter's life shown as vertical dashes. Grey shading indicates timing of closure to fishing for *C. auratus* from 1 Oct-31 Jan. †fish last detected on Shark Monitoring Network array 1 in Fig. 1; *fish recaptured at latitude 31° S.

**Fig. 6.** Frequency of occurrence of acoustic transmitters in tagged *Chrysophrys auratus* recorded at Site A between Garden and Carnac Islands (see Fig. 1) in each week of the spawning season in (a) 2010/11 and (b) 2011/12 relative to 1 Oct (Week 0 begins on 1 Oct when the fishing closure commences), with bimodal mixture models fitted to the frequency distributions. Mean weekly sea surface temperatures adjacent to Site A and mean weekly moon fraction (% full) shown above for the same period. Solid arrows identify where SSTs reached ~19 and 21°C and dashed arrow identifies the time of the November new moon (lowest moon fraction) in each year.
Fig. 7. Average percentage of the annual commercial and recreational sector catch of *Chrysophrys auratus* in each management area of the West Coast Bioregion; based on the average annual catch of the main commercial fishery (WCDSIMF) from 2008 to 2016 and the recreational sector catch, which combines catches of private vessels from the 2013/14 survey of Ryan et al. (2015) and the average annual charter vessel catch from 2008 to 2016.

Fig. 8. Monthly numbers of *Chrysophrys auratus* retained by charter fishers in 2015/16 in each 5nm × 5nm block of the Metropolitan Area of the West Coast Bioregion (31 - 33°S). \[%_{III/IV}\] = percentage of female *C. auratus* in each month with ovaries in pre-spawning (III) and spawning (IV) condition (created using reproductive data from Wakefield et al. 2015 with permission). Red shading indicates the spatial area closed to fishing for *Chrysophrys auratus* from 1 Oct-31 Jan. Nil catch in November is due to an annual closure to recreational fishing for demersal fishes in the West Coast Bioregion from 15 Oct–15 Dec (inclusive). Depth contours are 20, 50, 100, 200 m.

Fig. 9. Estimated number of private recreational vessels launched from Woodman Point boat ramp during each hour of the day (24 h clock) in each month in 2011/12 (from Ryan et al. 2013 with permission). Grey shading indicates closure to fishing for *Chrysophrys auratus* from 1 Oct-31 Jan. Bars on right show relative reproductive activity represented as percentage of female *C. auratus* in each month that contained ovaries in pre-spawning (III) and spawning (IV) condition (created using reproductive data from Wakefield et al. 2015 with permission).
Table 1. Results of adjusted Akaike Information Criterion (AICc) comparisons between single, bi- and tri-modal mixture distributions fitted to frequencies of occurrence of *Chrysophrys auratus* at Site A (Garden Island to Carnac Island pathway) during the 2010/11 and 2011/12 spawning seasons. \( n \) = sum of occurrence of *C. auratus* with transmitters per week between 1 Aug and 28 Feb. \( K \) = number of parameters estimated by the models.

<table>
<thead>
<tr>
<th>Spawning Season</th>
<th>( n )</th>
<th>Model</th>
<th>( K )</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010/11</td>
<td>68</td>
<td>Single mode</td>
<td>2</td>
<td>415</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bimodal</td>
<td>5</td>
<td>407</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tri-modal</td>
<td>8</td>
<td>412</td>
</tr>
<tr>
<td>2011/12</td>
<td>87</td>
<td>Single mode</td>
<td>2</td>
<td>516</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bimodal</td>
<td>5</td>
<td>503</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tri-modal</td>
<td>8</td>
<td>507</td>
</tr>
</tbody>
</table>

Table 2. Means (\( \bar{x}_1 \)) and standard deviations (\( s_1 \)) of bimodal mixture distributions fitted to frequencies of occurrence of \( n \) *Chrysophrys auratus* at Site A (Garden Island to Carnac Island pathway) during the 2010/11 and 2011/12 spawning seasons.

<table>
<thead>
<tr>
<th>Spawning Season</th>
<th>( n )</th>
<th>( \bar{x}_1, s_1 )</th>
<th>( \bar{x}_2, s_2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010/11</td>
<td>15</td>
<td>0.96, 2.34</td>
<td>9.57, 2.56</td>
</tr>
<tr>
<td>2011/12</td>
<td>12</td>
<td>0.57, 1.56</td>
<td>8.05, 3.22</td>
</tr>
</tbody>
</table>
(a) Water temperature (°C)

(b) Water temperature (°C)

Frequency of occurrence

1 Oct
31 Jan

https://mc06.manuscriptcentral.com/cjfas-pubs