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Remote underwater video for monitoring reef fish spawning aggregations

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Abstract

Fish spawning aggregations (FSAs) are critical events in the life cycle of many commercially and ecologically important species, yet FSAs are often exploited and highly vulnerable to fishing due to their predictability in time and space. Although FSAs are increasingly recognized as a conservation and management priority, monitoring these ephemeral dynamic events remains challenging. Here, we assessed the ability of remote underwater video (RUV) to monitor reef FSAs, using blacksaddled coral grouper (*Plectropomus laevis*) as a case study. We deployed RUV systems monthly on a year-round basis in a reef channel of the New Caledonian barrier reef where *P. laevis* was assumed to form spawning aggregations. Specifically, we investigated whether RUV could both track spatiotemporal changes in fish abundance and detect spawning signs to validate the purpose of potential gatherings. Our analysis revealed strong seasonal changes in *P. laevis* abundance, characterized by a 5-fold increase between October and February, and marked variations among sampled habitats. The probability of occurrence of males in courtship colouration showed spatiotemporal patterns fairly similar to those in abundance. Finally, we recorded clear courtship behaviours between November and April, providing evidence that *P. laevis* aggregate monthly to spawn during a protracted reproductive season. This study advances our understanding of the spawning aggregation dynamics of this understudied grouper, and highlights the potential of RUV to monitor and ultimately inform management of reef FSAs.

Keywords: remote underwater video; fisheries-independent survey; spawning aggregation; grouper; *Plectropomus laevis*; courtship behaviour; Coral Sea; New Caledonia

Introduction

Many animals form large, temporary aggregations for breeding in both terrestrial and marine ecosystems. This reproductive phenomenon, which is widespread in birds, mammals, reptiles, and fish, represents a critical event in the life cycle of the species that exhibit this behaviour (Erisman et al. 2017). Breeding aggregations generally occur at predictable times and specific locations (Domeier and Colin 1997; Yorio 2009). As a result, they are highly vulnerable to human pressures such as habitat degradation and harvesting and require adequate monitoring to support effective conservation and management (Parnell et al. 1988; Sadovy de Mitcheson et al. 2008; Shimada et al. 2021). This is particularly true for marine fish, whose spawning aggregations have been targeted by fishers for centuries (Johannes 1978) and have supported important commercial, recreational, and subsistence fisheries worldwide (Sadovy de Mitcheson and Erisman 2012). Fishers target fish spawning aggregations (FSAs) because a large number of fish can be caught in a relatively short amount of time. However, targeting fish aggregations can lead to the 'illusion of plenty' (Erisman et al. 2011), with catch rates remaining high while fish abundance declines. This hyperstability of catch rates has historically masked declines in exploited aggregating populations and contributed to collapses of commercial and recreational fisheries (Rose and Kulka 1999; Erisman et al. 2011; Hamilton et al. 2016). In response, FSAs have been increasingly protected by management measures such as seasonal fishing closures and permanent no-take marine reserves (Russell et al. 2012, Grüss et al. 2014), and are now recognized as a conservation priority (Sadovy de Mitcheson 2016; Erisman et al. 2017; Pittman and Heyman 2020), especially for long-lived, large-bodied, slow-growing, and/or late-maturing species that are highly vulnerable to fishing (Jennings et al. 1998, Jennings et al. 1999, Denney et al. 2002, García et al. 2008). Yet, many FSAs still lack any form of protection or monitoring and are in severe decline due to overfishing (Sadovy de Mitcheson et al. 2008; Russell et al. 2014; Chollett et al. 2020).

Monitoring FSAs is challenging due to their ephemeral and dynamic nature. Fishers' local ecological knowledge and fisheries-dependent data can provide a primary source of information on the location, timing, and temporal extent of exploited FSAs (Johannes et al. 2000, Colin 2012; Hamilton et al. 2012), but hyperstability of catch rates may preclude their use to investigate long-term changes in abundance (Sadovy and Domeier 2005; Erisman et al. 2011). In addition, fisheries-dependent data are lacking where FSA sites are seasonally or permanently closed to fishing. Alternatively, underwater visual censuses (UVCs) have been extensively used to study FSAs, particularly in coral reef ecosystems (e.g. Shapiro et al. 1993, Sala et al. 2001, Heyman and Kjerfve 2008, Rhodes et al. 2014). More recently, diver-operated stereo-video (stereo-DOV) (Salinas-de-León et al. 2015, Rastoin-Laplane et al. 2020) and laser callipers (Heppell et al. 2012; Stock et al. 2021) have also been used for this purpose. However, diver-based surveys involve time-consuming fieldwork, are subject
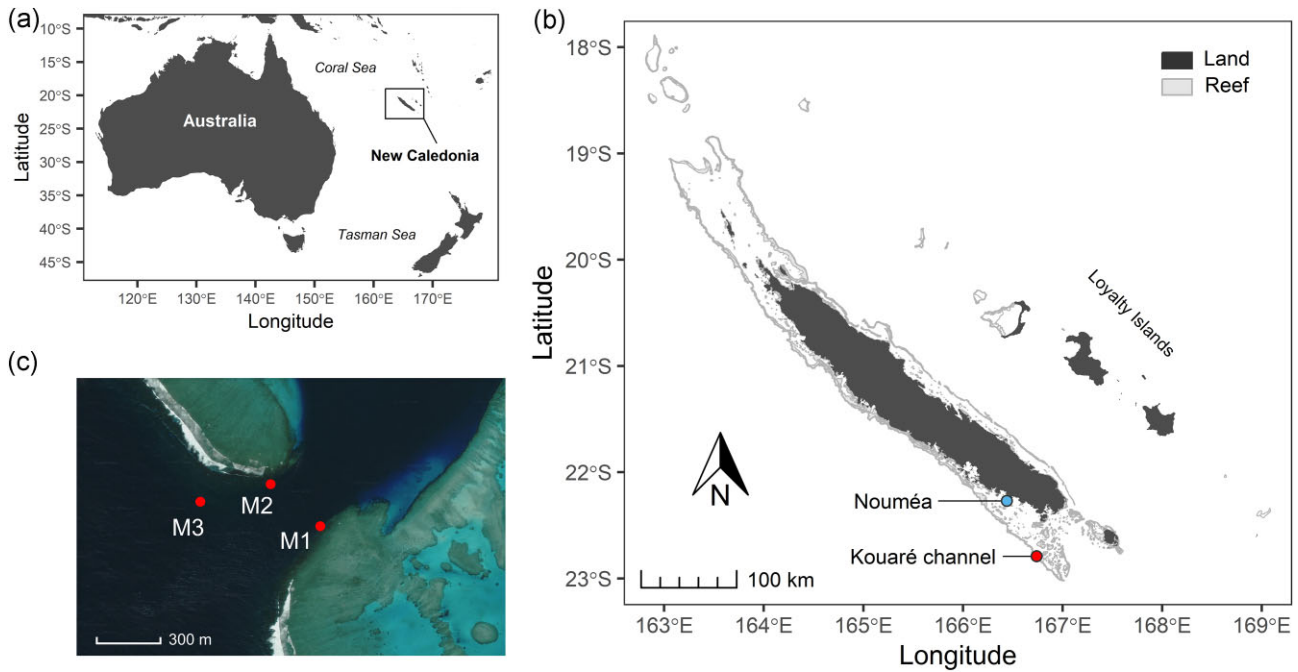
Figure 1. Study site in the Coral Sea (a, b) and sampling stations (M1, M2, and M3) at Kouaré channel (c). Imagery ©2024 CNES/Airbus, Maxar Technologies, Map data ©2024 Google.

to depth and time constraints, and may be precluded by weather conditions (e.g. strong currents). Furthermore, fish behaviour and thus fish counts can be affected by the presence of divers (Dickens et al. 2011; Lindfield et al. 2014). Limitations of fisheries-dependent data and diver-based surveys have led to repeated calls and ongoing efforts to develop alternative, fisheries-independent approaches for monitoring FSAs (Egerton et al. 2017; Rowell et al. 2017). Examples of such approaches include acoustic telemetry (Rhodes et al. 2012; Nemeth et al. 2023), and active (Taylor et al. 2006, Egerton et al. 2017) and passive (Rowell et al. 2012, 2019; Chérubin et al. 2020) acoustics. The potential of unbaited remote underwater video (RUV) for documenting FSAs was underlined long ago (Colin et al. 2003), but to date RUV has been used to validate or complement data collected with other sampling methods (e.g. Beets and Friedlander 1999, Binder et al. 2021), rather than as a stand-alone technique. Yet, RUV has proven useful for assessing spatiotemporal variations in relative fish abundance (Pelletier et al. 2012; Powell et al. 2016; Zarco-Perello and Enríquez 2019), and presents several advantages over alternative non-lethal methods. For example, RUV is less intrusive than UVC and stereo-DOV due to the absence of divers (Mallet and Pelletier 2014) and, unlike passive acoustics, is not limited to the study of sonorous species.

In the present study, we deployed RUV systems in a reef channel of the New Caledonian barrier reef that was assumed to host spawning aggregations of blacksaddled coral grouper (*Plectropomus laevis*), a large, commercially important grouper widely distributed in the Indo-Pacific (Heupel et al. 2010). This species is exploited in much of its range by hook-and-line, spear, and fish trap fisheries and represents a significant part of the live reef food fish trade (Choat et al. 2018). Like many other groupers, *P. laevis* is a solitary protogynous hermaphrodite (Sadovy de Mitcheson and Liu 2008; Frisch et al. 2016). Spawning aggregations of *P. laevis* have been much less studied than those of other coral groupers, no-

tably *P. leopardus* (Samoilys and Squire 1994; Samoilys 1997; Zeller 1998) and *P. areolatus* (Hamilton et al. 2011, Hamilton et al. 2012; Hughes et al. 2020; Sadovy de Mitcheson et al. 2020), even though anecdotal information can be found in the literature. *P. laevis* is known to form relatively small spawning aggregations (10s of individuals), in which reproductively active males display a temporary, distinctive courtship colouration (Sluka 2000; Sadovy de Mitcheson 2011; Choat et al. 2018). Currently, *P. laevis* is classified as least concern on the IUCN Red List, but fishery data are scarce and population trends are virtually unknown in most countries (Choat et al. 2018). Accordingly, the latest IUCN Red List Assessment recommends improving the monitoring of *P. laevis* fished populations and protecting their spawning aggregation sites (Choat et al. 2018). The objective of this study was twofold: (i) evaluate the capacity of RUV to identify and monitor FSAs by both tracking spatiotemporal changes in relative abundance and detecting undisputed spawning signs, using *P. laevis* as a case study, and (ii) advance our understanding of the spawning aggregation dynamics of this understudied coral grouper species.

Materials and methods

Study site

Kouaré channel is a 300 m wide, relatively deep (>20 m) barrier reef channel located off the southwest coast of New Caledonia in the Coral Sea (Southwest Pacific) (Fig. 1). This site is part of the Great Southern Lagoon, which was inscribed on the UNESCO World Heritage List in 2008 because of the exceptional diversity of its coral reefs and associated ecosystems. Typical underwater visibility ranges from 10 to 25 m in the reef channel. Fishing pressure at the study site is poorly known but is assumed to be relatively low, given that it is quite far (62 km) from the capital and largest city, Nouméa. Yet, Kouaré
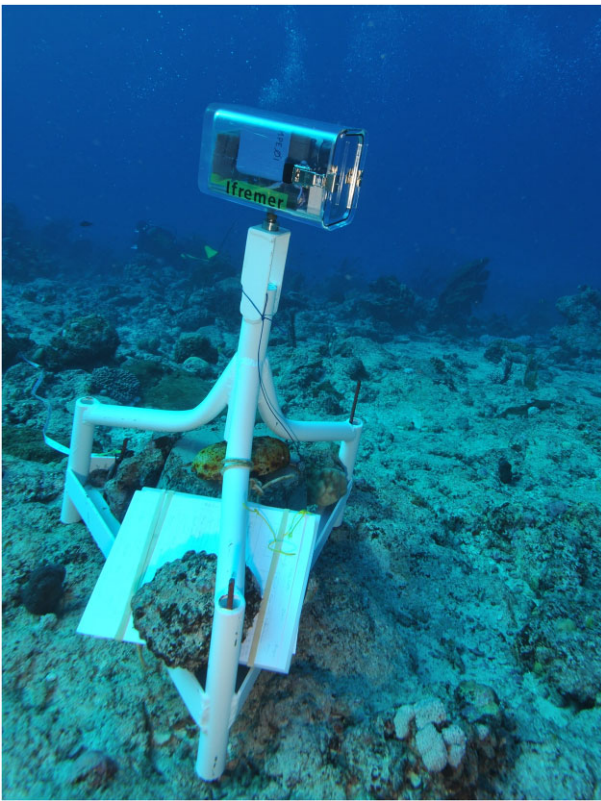
Figure 2. A MICADO system deployed at Kouaré channel, New Caledonia. The video camera enclosed in a waterproof housing was deployed monthly by a scuba diver and retrieved three days later, while the weighted tripod was left in place throughout the study period (11 months). Note that the diving slates placed on the tripod were retrieved by the diver after the photo was taken. Photo © M. Juncker.

channel is an important fishing ground for local communities and for recreational fishing. This site was chosen based on interviews with local fishers and previous UVC surveys, which suggested that *P. laevis* aggregate to spawn at Kouaré channel (Juncker and Lamand 2009; Imirizaldu 2012). No specific management measure has been established in the area to date.

Data collection

Fish data were collected on a year-round basis using an unbaited rotating RUV system named MICADO (Fig. 2). Each month between August 2014 and June 2015, a MICADO was deployed around the full moon by a scuba diver and left in place for 3 days at three different fixed sampling stations (Fig. 1c). Stations M1, M2, and M3, located at depths of 20 m, 14 m, and 17 m, respectively, were representative of three contrasting habitats where *P. laevis* were thought to potentially aggregate to spawn (see Suppplementary Text S1 for a detailed description of each station). Field surveys were conducted around the full moon as *P. laevis* were reported to form spawning aggregations around this lunar phase in New Caledonia (C. Chauvet, personal communication).

The MICADO system consists of a high definition video camera enclosed in a waterproof housing attached to the top of a weighted tripod, with an motor to rotate the camera housing, and a timer to switch the system on and off at predefined time intervals, which ranged from 06:00 a.m. to 05:30 p.m. (i.e. daylight hours) in the present study (Fig. 2, Supplemen-

tary Fig. S1). This RUV system is the programmable version of the STAVIRO (Mallet et al. 2016; Pelletier et al. 2021). When the MICADO is switched on by the timer, the motor rotates the camera housing by 60° every 30 seconds. A complete (360°) rotation thus takes ∼3 minutes. Each video includes three complete rotations.

After fieldwork, all fish observed during each rotation within a 10 m radius around the MICADO were counted by a trained analyst, resulting in three fish counts per video. A MeanCount or MaxN approach (Ellis and DeMartini 1995; Schobernd et al. 2014) was not used in this study because the relatively low number and mobility of aggregating fish enabled us to count all individuals observed during a given rotation, with a low risk of double counting. Nevertheless, particular attention was given to the direction of fish movement with respect to camera rotation, and any individual suspected to have already been observed was not counted (Pelletier et al. 2012, 2021; Mallet et al. 2016). The 10 m radius around the MICADO corresponded to the poorest underwater visibility encountered at the study site; its estimation in each video was conducted by an analyst trained with reference images containing bright and dark fish silhouettes of different sizes, filmed at different known distances and under different underwater visibility conditions (Pelletier et al. 2021). Unambiguous spawning signs (e.g. courtship colouration and behaviours) were also recorded to validate the nature of potential gatherings. On average, 6, 9, and 4 videos per day were analysed at stations M1, M2, and M3, respectively, with variations between days and months at each station and between stations (Supplementary Fig. S1, Text S2).

Fish counts from RUV were supplemented by fish length data from stereo-DOV collected opportunistically from December to June when MICADOs were deployed and/or retrieved. The stereo system was calibrated using CAL software and the measurements were obtained from EventMeasure software (https://www.seagis.com.au/). Tide data recorded at Numbo station (in Nouméa) were obtained from the SHOM data portal (http://data.shom.fr).

Statistical analysis

We used generalized linear mixed models (GLMMs) to investigate spatiotemporal changes in (i) relative abundance (number of fish per rotation) and (ii) the probability of occurrence of males displaying a courtship colouration (hereafter referred to as 'coloured males'). We used a Poisson distribution with a log link to quantify relative abundance and a binomial distribution with a logit link to model the probability of occurrence of coloured males. We focused on the probability of occurrence rather than the abundance of coloured males, because no more than one coloured male was generally observed in a given rotation. Month (categorical, eleven levels), sampling station (categorical, two levels), time of day (categorical, five levels), and tidal height (continuous) were included as fixed effects in the GLMMs. Video identity was included as a random effect in all models to account for the dependency among observations from the same video. The full models contained two-way interactions between sampling station and each of the other fixed effects. Prior to analyses, the continuous covariate 'tidal height' was standardized by subtracting its mean and dividing by its standard deviation to facilitate comparison of effects' size among covariates. We checked for multicollinearity using the *check_collinearity* function of

the R package 'performance' (Lüdecke et al. 2021), and ensured that all covariates included in a single model had variance inflation factors <3. Although we initially considered the number of Days After the Full Moon (DAFM) as a potential covariate, it was not retained in the analyses because of its collinearity with the 'month' covariate (due to logistical constraints, RUV systems were deployed 11 DAFM in January and [-2; 4] DAFM the other months). Video analyses revealed that very few individuals (Supplementary Fig. S2) and no coloured males were observed at station M3. To address this issue and avoid complete separation in binomial GLMMs, we fitted Poisson and binomial GLMMs to a restricted dataset excluding station M3. Model selection was conducted by automatically ranking models using the Akaike's information criterion corrected for small sample size (AICc) and the *dredge* function of the R package 'MuMIn' (Bartoń 2023). Models with a ΔAICc ≤2 were considered competitive models with similar support from the data (Burnham and Anderson 2002). When competitive models were present, the most parsimonious model was conservatively selected as the 'best' model. We quantified the variance explained by the fixed effects (marginal R^2) and that explained by both fixed and random effects (conditional R^2) for each best model using the *r.squaredGLMM* function of the R package 'MuMin'. We assessed dispersion, zero-inflation and patterns in the residuals using the R package 'DHARMa' (Hartig 2022) (Supplementary Figs. S3–S6).

Finally, we performed a sensitivity analysis to test whether variations in sampling effort among stations could have influenced our results. In particular, we investigated whether the very low abundance recorded at station M3 could have resulted from the lower number of videos available at that station (Supplementary Figs. S1 and S2). To do so, we refitted the best Poisson and binomial GLMMs to a subset of data that included only those collected at stations M1 and M2 at the dates and times they were available at station M3.

We did not investigate spatiotemporal changes in fish length because length data were collected using an unstandardized sampling procedure. However, we compared the length-frequency distribution to lengths at 50% and 95% female maturity and those at 50% and 95% sex change available in the literature (Heupel et al. 2010). Prior to the comparison, fork lengths from the literature were converted to total lengths (TL) using a mean conversion factor from FishBase (Froese and Pauly 2024). All analyses were conducted using R version 4.3.2 (R Core Team 2023).

Results

Spatiotemporal variations in relative abundance
Relative abundance of *P. laevis* ranged from 0 to 15 individuals per rotation, with large variations between stations and months (Fig. 3a and b and Supplementary Fig. S2). Large variability in relative abundance was also observed among and, to a lesser extent, within (i.e. from one rotation to the other) videos recorded the same day at a given station.

The best Poisson GLMM included the effects of month, station, time of day, and tidal height (Fig. 4); together, they explained 47% of variability in the data (marginal $R^2 = 0.47$, conditional $R^2 = 0.56$). Two models including an interaction term between month and station received similar support

(Supplementary Table S1), but they did not explain more variance than the best model. The 'month' covariate had by far the greatest effect on relative abundance (Fig. 4), followed by station, time of day, and tidal height. Relative abundance of *P. laevis* showed a strong seasonal pattern characterized by a 5-fold increase between October and February, and was about three times higher at station M1 than at station M2 (Figs. 3 and 4). At station M2, relative abundance in January was strikingly lower than that in December and March. Clear diurnal variations were also detected, with relative abundance being lower in the early morning and late afternoon, and peaking at midday (Fig. 4). Tidal height had a small positive effect on relative abundance. Fitting the best Poisson GLMM to a restricted dataset mimicking data availability at station M3 led to fairly similar standardized coefficient estimates but larger 95% confidence intervals (Supplementary Fig. S7).

Spatiotemporal variations in courtship coloration
Males *P. laevis* observed at Kouaré channel exhibited a distinctive courtship colouration characterized by an almost black body, speckled white forehead and midbody areas, and generally, light-coloured lips and white pelvic fins bordered in black (Fig. 5). Coloured males were observed throughout the sampling period at stations M1 and M2; however, their occurrence strongly varied between months and stations (Fig. 3). The best binomial GLMM included the effects of month, station, and time of day (Fig. 4, Supplementary Table S2), which together explained 52% of variability in the data (marginal $R^2 = 0.52$, conditional $R^2 = 0.65$). Overall, the probability of occurrence of coloured males followed fairly similar variations in time and space to those observed in relative abundance (Figs. 3 and 4). These variations were characterized by (i) a strong seasonal pattern, with probabilities of occurrence ≤10% in August–September and May–June, and as high as 80% in February at midday at station M1, (ii) a diurnal pattern, with a peak at midday, and (iii) a mean probability of occurrence four times higher at station M1 than at station M2. Similar to what was observed for relative abundance, month had the greatest effect on the probability of occurrence of coloured males, followed by station and time of day (Fig. 4). One, two, or three males were observed in 74%, 19%, and 4% of the video rotations, respectively, in which coloured males were encountered. On three occasions (one in November, one in December, and one in February), up to five distinct males were observed in a given rotation at station M1. In addition to coloured males, many individuals exhibited another distinctive colour pattern characterized by a dark head extending from the snout to the preoperculum, a more or less pale body, and dark margins on all fins (Fig. 5b). The frequency of occurrence of pale phase individuals was not recorded. Fitting the best binomial GLMM to the subset of data mimicking data availability at station M3 led to complete separation, which resulted in unrealistically large parameter estimates and standard errors (not shown). However, this restricted dataset contained 47 and 12 video rotations with at least one coloured male observed at stations M1 and M2, respectively.

Courtship behaviours
Unambiguous courtship behaviours were observed each month (except January) from November 2014 to April 2015, mostly at station M1. In particular, intense courtship activity was recorded at this station on November 7 (full moon)
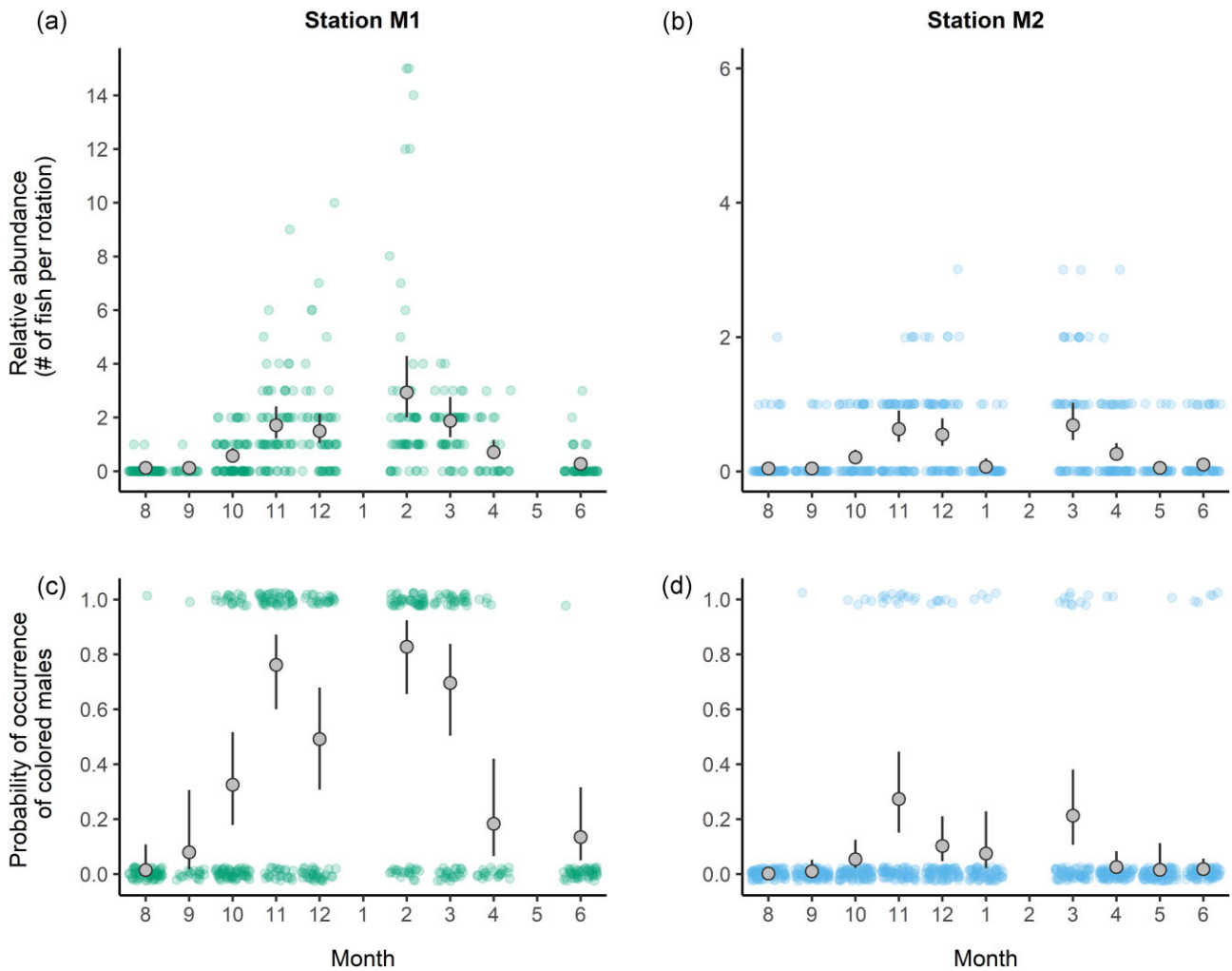
Figure 3. Relative abundance (number of fish per rotation, a, b) and probability of occurrence of coloured males (c, d) throughout the sampling year at stations M1 (left panels) and M2 (right panels). Grey dots represent GLMM predictions at midday (averaged over tidal height for relative abundance), and solid bars their 95% confidence intervals. Coloured dots represent continuous (relative abundance) and binary (presence = 1, absence = 0) raw data, which are slightly jittered for clarity (green: station M1, blue: station M2). Note that some solid bars are small relative to the size of the dots, and the y-axis scale differs between plots (a) and (b). GLMM predictions were not displayed where the data were missing (e.g. at station M2 in February).

and December 9 (3 days after full moon), 2014, where many successive courtship behaviours were observed at midday within <10 minutes. Courtship behaviours typically involved a coloured male quickly approaching a normal or pale phase individual, presumed to be a female, while shaking its head and body for short bursts (Fig. 5c–f; see also the video openly available at https://doi.org/10.24351/101975). Coloured males were also observed following normal and pale phase individuals, and occasionally performing lateral display, which consisted of swimming slowly with the body lateral to the seafloor and the back or the belly facing the targeted individual. Gamete release was not observed following courtship behaviours. No courtship behaviour was recorded at station M3.

Length-frequency distribution from stereo-DOV

A total of 59 individuals observed in stereo-DOV were successfully measured. The lengths of *P. laevis* ranged from 54 to 110 cm TL (mean TL = 78 cm), 100% and 78% of which were above the length at 50% and 95% female maturity, re-

spectively. The length-frequency distribution appears to be bimodal, with a boundary between the two modes close to but likely slightly smaller than the length at 95% sex change (Fig. 6).

Discussion

Spawning aggregation dynamics of blacksaddled coral grouper

Our analysis showed that *P. laevis* aggregated to spawn at Kouaré channel each month from November to April, as indicated by the higher relative abundance and probability of occurrence of coloured males, as well as monthly observations of courtship behaviours during this 6-month period, which corresponds to the warm, wet season in New Caledonia (Specq et al. 2020). Seasonal patterns in relative abundance and in the probability of occurrence of coloured males further suggest that spawning may have started as early as October, and peak spawning occurred from November to February. Histological analysis of gonads would be required to confirm the begin-
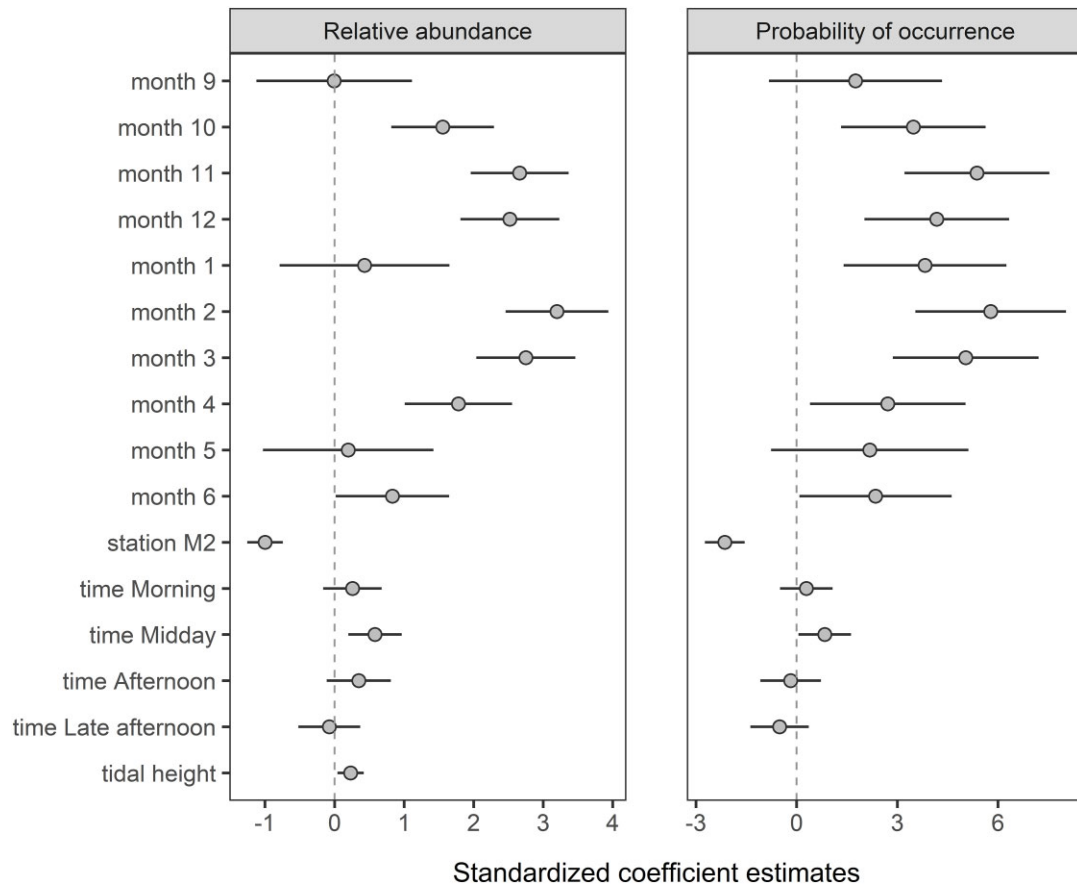
Figure 4. Standardized coefficient estimates (dots) and 95% confidence intervals (solid bars) for the best GLMM for relative abundance (Poisson GLMM, left panel) and the probability of occurrence of coloured males (binomial GLMM, right panel). Note that the x-axis scale differs between the two plots.

ning and end of this protracted reproductive season, which is slightly longer than that reported for the same species in northeastern Australia (Heupel et al. 2010) and similar to that of other coral reef fishes, including groupers, snappers, and parrotfishes in New Caledonia (Flynn et al. 2006, Moore 2019, 2022).

The sampling design did not allow us to quantify the influence of the moon on the abundance and spawning behaviour of *P. laevis*. However, the low abundance of the species and the low probability of occurrence of coloured males recorded 11 DAFM in the middle of the spawning season (January) strongly suggest that *P. laevis* spawns a few days before and/or after the full moon at Kouaré channel, and progressively disperses after spawning. At Dumbéa, another reef channel located ∼70 km northwestward off Nouméa, *P. laevis* was reported to spawn the last 2 days before the full moon (C. Chauvet, personal communication). Given that RUV systems were generally deployed during or a few days after the full moon, the low number of individuals with a swollen abdomen at Kouaré channel, combined with the reported observations at Dumbéa, further suggests that *P. laevis* spawns a few days prior to, rather than after the full moon in New Caledonia. This may explain why no spawning event (gamete release) was observed in the videos, despite the high sampling frequency and the large range of sampling hours. The limited vertical field of view of RUV systems deployed on the seafloor may also have precluded the observation of spawn-

ing if it occurred high in the water column, as reported for some grouper species (e.g. Samoilys and Squire 1994, Rowell et al. 2019). The similar diurnal patterns in relative abundance and in the probability of occurrence of coloured males suggest that *P. laevis* individuals were more numerous and more active around midday and either dispersed or hidden within the reef during the rest of the day, in accordance with previous findings on *P. laevis* movement patterns (Matley et al. 2016). An alternative hypothesis could be that *P. laevis* moved to shallower or deeper waters during crepuscular periods to actually spawn, but to our knowledge this behaviour has not been observed in this species. *P. laevis* activity also appears to be influenced by tidal height (Matley et al. 2016). The number of fish detected by RUV is likely to depend, at least in part, on fish movements (Follana-Berná et al. 2020), which may explain the small positive effect of tidal height on *P. laevis* relative abundance found in the present study. Although the underlying mechanism remains unknown, it is unlikely to be related to courtship or spawning, as we found no effect of tidal height on the probability of occurrence of coloured males.

Since coloured males performed clear courtship behaviours toward pale phase individuals, the latter were likely to be females. To our knowledge, this pale colouration has not been previously documented and should be further investigated to determine if it is only displayed by females and is exclusively associated with courtship and spawning. The bimodal length-
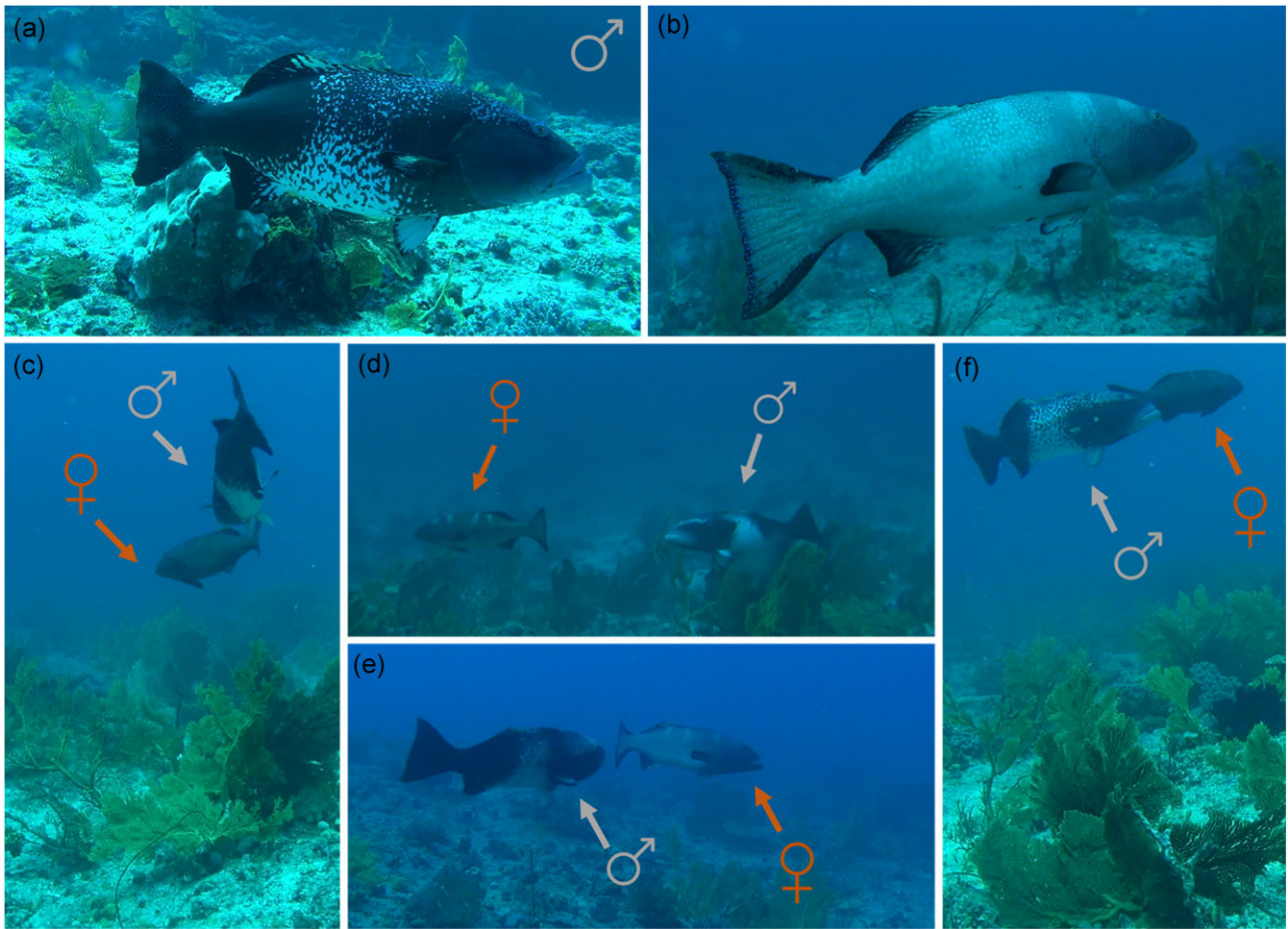
Figure 5. Courtship colouration of a male (a) and presumably a female (b) *P. laevis*; (c–f) examples of courtship behaviours recorded at Kouaré channel. Photo © E. Saulnier.
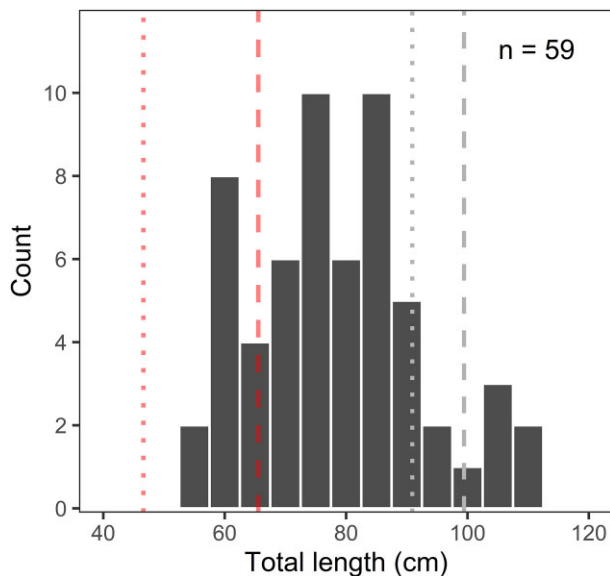
Figure 6. Length-frequency distribution of *P. laevis* observed in diver-operated stereo-video. The vertical red and grey lines represent the lengths at 50% (dotted) and 95% (dashed) female maturity and sex change, respectively.

frequency distribution, characterized by very few individuals above the length at 95% sex change, revealed that the sex ratio of the aggregation was strongly biased toward females, as expected for monandric, protogynous hermaphrodites such as *P. laevis* (Adams 2003). The fact that all fish were above the length at 50% female maturity further indicates that most individuals encountered at Kouaré channel were sexually mature.

Understanding why *P. laevis* individuals were more numerous and courtship activity more intense at station M1 than at stations M2 and M3 is beyond the scope of the present study. However, these findings confirm that *P. laevis* spawning aggregations occur at very specific locations, even at the scale of the reef channel. Together, our results suggest that the *P. laevis* spawning aggregation observed at Kouaré was likely composed of several fish groups, each including few males and more numerous females, located on both sides of the reef channel. *P. laevis* abundance reported in this study was likely much lower than the real number of fish that could have been theoretically observed during the peak spawning period due to the high complexity of reef habitats (fish potentially hidden within the reef), the fairly late deployment of RUV systems relative to the full moon, and our conservative approach in counting fish (see methods). Given that up to 15 individuals were concurrently observed within a small sampling area

(10 m radius around the camera), and considering the size of the reef channel (its southern side is >700 m long), the total number of *P. laevis* aggregating simultaneously at Kouaré channel might be much larger than the size of previously reported spawning aggregations formed by this species (30–50 individuals, Sadovy de Mitcheson 2011, Choat et al. 2018). Determining the absolute size (number of fish) and spatial extent of this aggregation would require further investigation.

RUV: a useful yet underused tool for monitoring FSAs

Previous applications of RUV at FSA sites have been limited to validating or supplementing data collected with other sampling techniques, such as fish traps, UVC, and passive acoustics (Beets and Friedlander 1999; Schärer et al. 2012; Sadovy de Mitcheson et al. 2020; Binder et al. 2021). In the present study, we followed the opposite approach, using RUV as the primary sampling tool to collect data on fish abundance and behaviour, supplemented by fish lengths from opportunistic stereo-DOV. In addition to detecting indirect spawning signs, RUV has proven capable of tracking spatiotemporal variations in the relative abundance of *P. laevis*, a naturally rare species (density often < one individual per 1000 m^2) that forms relatively small spawning aggregations (Choat et al. 2018). Thus, RUV is likely to be suitable for documenting and monitoring FSAs formed by many other aggregating fish species, particularly those that are more abundant and/or form larger spawning aggregations. Baited RUV has been successfully used to quantify interannual variation in the relative abundance of several reef-associated fish species (Bacheler and Ballenger 2018; Bacheler et al. 2022, 2023); unbaited RUV could be used for the same purpose at FSA sites, although it remains to be tested. It is also particularly suitable for documenting fish spawning behaviours, which may be disrupted by the presence of divers (Colin et al. 2003, Heyman et al. 2010) or the use of bait. RUV systems can be deployed in locations where depth or challenging underwater conditions (e.g. strong currents) preclude diver-based surveys. Another important advantage of RUV is the relatively low field effort required to implement a high sampling frequency (e.g. up to 12 videos per day for 3 consecutive days in the present study), which allows the investigation of fine-scale spawning aggregation dynamics. This could be particularly helpful in determining when to conduct broader spatial surveys to estimate the spatial extent of the FSA and/or the total abundance of fish within the aggregation. The duration of the monthly RUV deployments at Kouaré channel was limited by the battery life and storage capacity of the MICADO, but the temporal resolution of RUV surveys can now be significantly improved using more recent video cameras with extended recording capabilities. A downside of stationary RUV systems such as the MICADO is their limited vertical field of view and the relatively limited area sampled by a given device. These limitations could be overcome by deploying more RUV systems than in this study or, alternatively, more sophisticated systems with hemispherical or multi-camera rigs. The metric used as an index of abundance should also be carefully chosen based on the size of the aggregations formed by the studied species. If the estimation method used here worked well to document a relatively small aggregation (10s of fish), a MeanCount or MaxN approach would be more appropriate for counting fish that form larger FSAs (100s-1000s). RUV can also be useful for tracking the arrival and departure of fish at the FSA site, regardless of the size and density of the aggregation. In any case, preliminary surveys (e.g. UVC, interviews with fishers) are required or at least recommended prior to the deployment of RUV systems to identify locations where FSAs are known or likely to occur, as was the case in this study. It should also be noted that RUV, like all visual techniques, can only be used in locations with sufficient underwater visibility. A last potentially important limitation is the time required for trained observers to analyse numerous videos. However, this amount of time can now be drastically reduced thanks to recent advances in automated image analysis using machine learning algorithms (e.g. Villon et al. 2018, Sheaves et al. 2020, Connolly et al. 2021, Fleuré et al. 2024). Each sampling technique for surveying FSAs has its own advantages and limitations (Colin et al. 2003). Depending on the purpose of the study and the logistical resources available, RUV may be used alone or in combination with additional sampling devices. Here, RUV was sufficient to confirm that *P. laevis* aggregated to spawn at Kouaré channel, highlighting its strong potential for studying FSAs, but we encourage the use of complementary techniques whenever possible to comprehensively document reef FSAs (e.g. acoustic-optical survey). Synchronous in-water observations using different visual techniques such as RUV and UVC would also be useful to compare their respective performance in assessing reef FSAs.

Implications for conservation and management

P. laevis has been heavily exploited in parts of its geographical range, and population declines have occurred in some locations, including the Maldives, the Solomon Islands, and Indonesia (Scales et al. 2007, Choat et al. 2018). Due to the significant local risk of ciguatera poisoning, *P. laevis* is not targeted in New Caledonia, although fished individuals can be found for sale at the largest local seafood market in Nouméa (Clua et al. 2011). For this reason, fishing mortality of *P. laevis* is thought to be relatively low in New Caledonia, or at least lower than that of *P. leopardus,* which presents a lower risk of being ciguatoxic (Clua et al. 2011). However, fishing mortalities of both species remain unassessed. Furthermore, recent evidence suggests that *P. laevis* has a slower growth rate, larger sizes at maturity and sex change, and a longer life span than other coral groupers, notably *P. leopardus* (Heupel et al. 2010; Payet et al. 2020). All these life-history traits are generally associated with greater vulnerability to fishing and a lower potential to recover (Jennings et al. 1998, Denney et al. 2002). Following the recommendations of the most recent IUCN Red List Assessment (Choat et al. 2018), and given the lack of knowledge on local population status and trends, implementing a seasonal fishing closure at Kouaré channel during the peak spawning season of *P. laevis* could be a useful precautionary management option, combined with the adoption of a monitoring program to gather more data on grouper dynamics. Some FSA sites are used for spawning by multiple species (e.g. Heyman and Kjerfve 2008, Rhodes et al. 2014), and interviews with local fishers and previous UVC surveys suggest that this may be the case at Kouaré channel (Juncker and Lamand 2009; Imirizaldu 2012). A seasonal closure could thus protect spawning aggregations formed by several species in addition to *P. laevis,* and benefit many reef fishes that use this reef channel for purposes other than spawning. A similar management measure was implemented in 2005 at Dumbéa

channel, known as a multispecies FSA site, which has since been closed to fishing annually from October to March. Further investigations are strongly recommended to assess the size and spatial extent of the *P. laevis* aggregation at Kouaré channel, and to investigate whether other reef species aggregate in the same area either simultaneously or sequentially, to design appropriate management measures. Videos such as those collected in this study would usefully support the discussion and development of management options with local fishers and managers and foster their acceptance and compliance.

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Author contributions

Erwan Saulnier: Conceptualization, Methodology, Data curation, Software, Formal Analysis, Writing—original draft, Writing—review & editing. Annette Breckwoldt: Project administration, Conceptualization, Writing—review & editing. Marianne Robert: Conceptualization, Methodology, Writing—review & editing. Dominique Pelletier: Project administration, Conceptualization, Methodology, Investigation, Funding acquisition, Writing—review & editing.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

The survey data used in this study will be shared on reasonable request to the corresponding author. The tide data are openly available in the SHOM data portal at http://data.shom.fr. A video providing an overview of courtship behaviours recorded at Kouaré channel is openly available in the Océanothèque repository at https://doi.org/10.24351/101975.

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