Drivers and implications of change in an inshore multi-species fishery

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Inshore fisheries are an important source of employment and income across Europe. However, their sustainability and management efficacy are relatively understudied, particularly in a multispecies context. Management of these data-limited fisheries can be informed by assessments of standardized catch and landings per unit effort (CPUE and LPUE) data from fishery-dependent surveys. We demonstrate the utility of this approach in the first robust assessment of the sustainability and management of a multispecies inshore fishery for live wrasse (Labridae) in southern England. Our findings have wider ramifications for assessment and management of inshore fisheries, including international live wrasse fisheries, many of which are intensely exploited but have less stringent management than the fishery studied here. Using generalized linear models, we identified ecologically relevant drivers of variation in CPUE and LPUE, alongside interspecific variation in responses to fishing pressure during 2017–2019. We also highlight robust evidence of declines in the primary target species, a protogynous hermaphrodite, that are suggestive of fishery impacts driven by management-enabled selective removal of mature females. We demonstrate the need to consider ecologically similar species separately for management purposes, and account for ecogeographical variables in assessments; a failure to do so risks erroneous conclusions regarding inshore fisheries’ sustainability.

Keywords: generalized linear models, Labridae, live wrasse fishery, multispecies fishery management, selective harvesting, standardized CPUE, standardized LPUE

Introduction

European inshore fisheries are important sources of employment and income, and comprise around 80% of the fleet (Macfadyen et al., 2011). Despite this, the management and sustainability of inshore fisheries are relatively understudied, with limited monitoring of catches and effort. Sustainable management is made increasingly difficult by this sector’s ability to diversify more quickly than management can adapt, exploiting multiple species through changing technology, new market niches and flexibility in time spent fishing (Symes and Phillipson, 2013).

An understanding of stock dynamics is essential in developing fisheries management strategies. However, many inshore fisheries are poorly sampled by traditional fishery-independent survey techniques, and have insufficient data to develop complex stock assessments or estimates of Maximum Sustainable Yield, which is often seen as the core focus of sustainable fisheries management (Ricker, 1975; Hilborn and Walters, 1992; Lart, 2019). Alternatively, standardized catch and landings per unit of effort (CPUE and LPUE) data from fishery-dependent surveys can provide a relatively quick assessment of stock abundance dynamics (Metri and Perez, 2014) and accounts for the impact of spatial and environmental variables on catch rates, allowing for a more accurate representation of stock dynamics over time (Maunder and Punt, 2004; Venables and Dichmont, 2004). Although this approach does present some challenges, it can also permit identification of the variables that influence catch rates, providing

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information on the ecology of the target species that can inform management decisions (Maunder and Punt, 2004).

Since the early 1970s, inshore fisheries have developed in the United Kingdom, Norway, and Ireland for several wrasse species, namely: ballan (Labrus bergylta), corkwing (Symphodus melops), goldsirnny (Centrolabrus rupestris), rock cook (Centrolabrus exoleucus), and cuckoo (Lasius mixtus) wrasse. These species are captured live for use as a biological control mechanism for the control of ectoparasites (Copepoda, Caligidae) in farmed Atlantic salmon (Salmo salar; Sayer et al., 1996b; Bjordal, 1988). These cleanerfish are routinely being used in salmon aquaculture, with several million used each year in Norway alone (Skiftesvik et al., 2014a) and tens of thousands being removed from small geographic ranges on the south coast of England (Riley et al., 2017; Supplementary Appendix S1). Although wrasse are an efficient method for parasite treatment in the aquaculture sector (Bjordal, 1988; Skiftesvik et al., 2013), ongoing removal of large numbers of fish from wild populations poses questions regarding the sustainability and potential impacts of such exploitation on wild stocks.

The respective management authorities have implemented management measures in an attempt to improve sustainability in these fisheries while accounting for the biology, behaviour, and ecology of the targeted wrasse species. The measures implemented include combinations of some or all of: closed seasons and areas, size restrictions, fishing gear and vessel limitations, and quotas (SIFCA, 2017; CIFCA, 2018; Norwegian Directorate of Fisheries, 2020; Townsend, 2020). In the English fisheries, these measures seek sustainability by aiming to maintain wrasse stocks and their ecological functions, particularly within the relevant Special Areas of Conservation (Natural England, 2020). As a result, live wrasse fisheries are some of the most highly regulated inshore fisheries in Europe.

Although extensive regulations are in place, there has been limited effort to assess their efficacy at ensuring the sustainability of the fisheries, which is in part due to the relative difficulty of defining and assessing sustainability for such a fishery. First, there are currently no widespread, robust stock assessments for the wrasse species, even where catch quotas exist. Previous dedicated monitoring of wrasse abundance has investigated the distribution of multiple species across different habitat types where no fishery existed at the time of sampling (Sayer et al., 1993; Skiftesvik et al., 2014a,b), or has compared fish and unfished locations in Norway without considering inter-annual changes in catch, or the influence of environmental variables (Halvorsen et al., 2017). Furthermore, sampling trips for stock assessments of other commercial species do not sufficiently sample the rocky inshore habitats that wrasse inhabit (Metri and Perez, 2014). The multispecies nature of the live wrasse fisheries adds a further level of complexity to assessments of their sustainability. The target species likely have different relationships between fishing pressure and abundance due to their differing life-history traits (Darwall et al., 1992; Skiftesvik et al., 2014b; Supplementary Appendix S2), adding further complexity to assessments of sustainability of the fishery as a whole.

In southern England, the Inshore Fisheries and Conservation Authorities (IFCAs; the management authorities for inshore fisheries in England) use annual monitoring of the live wrasse fishery to generate evidence to support adaptive management. For example, using data from fishery-dependent observer surveys, Curtin et al. (2020) highlighted significant declines in both CPUE and LPUE of rock cook between 2017 and 2019 in the Devon & Severn IFCA’s (DSIFCA) district. On this basis, DSIFCA altered the potting permit bylaw to prohibit removal of rock cook from the fishery (DSIFCA, 2020). However, these analyses were not based on standardized CPUE and LPUE (i.e. did not consider changes in relation to spatial and environmental variables).

Here, we use a live wrasse fishery in Plymouth Sound (SW England) as a case study to investigate:

(i) whether there is temporal variation in standardized wrasse CPUE and LPUE,
(ii) key environmental and spatial drivers of CPUE and LPUE, and
(iii) suitability of current (and past) management measures in ensuring the sustainability of the fishery.

The relatively constrained geographic range of the Plymouth Sound fishery, limited number of vessels and relatively high levels of monitoring by the IFCAs (Curtin et al., 2020), provided an opportunity to deliver a detailed and robust assessment of the sustainability of this fishery, which will be valuable in developing appropriate management measures and predicting potential impacts of inshore fisheries elsewhere.

Material and methods

Study system—Plymouth Sound

Plymouth Sound is an embayment on the south west coast of England with a steeply sloping rocky coastline to the east and west. The bay encompasses diverse communities and habitats, including intertidal and subtidal limestone reefs and subtidal sediments. The inner Sound is sheltered by an artificial breakwater, and the main freshwater input is provided by the River Tamar in the northwest (Figure 1).

A live wrasse fishery developed in Plymouth Sound in early 2015, and the relevant IFCAs became aware of the fishery in 2016. The fishery comprises four to five vessels per year, each ranging from 5 to 8 m in length. The majority of fishers’ fish within both Cornwall IFCA (CIFCA) and DSIFCA’s districts (Figure 1), but data protection requirements prevent reliable matching of anonymized vessel identities. Fishers set strings of wrasse pots (Carapax; Lysekil, Sweden) in varying numbers, typically baited with crabs or bait balls to attract wrasse. Pots are designed to exclude bigger fish and are fitted with escape gaps to allow smaller wrasse to escape (Supplementary Appendix S3). Fishers in Plymouth Sound target all species of wrasse (except cuckoo), and land all individuals within the size restrictions (Supplementary Appendix S3). Differences in fishing practices between vessels relate to fisher preferences for location, soak time (deployment duration) and bait. Wrasse landings in the Plymouth Sound fishery are contextualized relative to other live wrasse fisheries in Supplementary Appendix S1.

Management of the live wrasse fishery in Plymouth Sound

Both CIFCA and DSIFCA have developed management measures for the live wrasse fishery in their districts, including minimum and maximum conservation reference sizes (CRSs) for retained wrasse, closed fishing seasons and closed areas. Supplementary Appendix S3 provides details of all management measures and how they have been modified over time, based on evidence...
collected by IFCA staff. The main differences between the two district’s management measures are the closed seasons (the main fishing season opens 15 days later in the DSIFCA district; Supplementary Appendix S3), and the CRSs for ballan (CIFCA: 16 cm +, DSIFCA: 15–23 cm) and corkwing wrasse (CIFCA: 12 cm +, DSIFCA: 14–18 cm).

Data collection
Fisheries data
Data were collected during observer surveys of commercial fishing operations between April and December in 2017–2019. Survey effort for each month varied between years so, to reduce sampling bias, we only used data from months that were surveyed in all years (July–October). For each survey, the date, time, bait type, soak time (number of nights the gear was set for) and fishing locations (start and end points of each string) were recorded. Each wrasse caught was identified to species level and total length measured to the nearest 0.5 cm, with those outside the CRS range immediately returned to the sea. Supplementary Appendix S1 outlines additional fisheries data collection (fishers self-reported fishing locations and effort, and wrasse sales notes data) provided as context for this fishery.

Supporting environmental and geographic covariates
We calculated maximum tidal range (TR) for every day during 2017–2019, using observed maximum and minimum sea levels provided by the British Oceanographic Data Centre (BODC, 2020). Bathymetric data for Plymouth Sound (grid resolution ~115 m) were obtained from the EMODnet Bathymetry Consortium Digital Terrain Model (EMODnet, 2020), with water depths relative to the Lowest Astronomical Tide Datum. We used these data in QGIS (2020) to calculate the mean depth of the start and end of each string of pots. Strings are not always laid in a straight line, and may vary in depth across the length of the string; each string was therefore assigned to a 5-m depth band between 0 and 15 m, with an additional depth band for areas >0 m, which are intertidal on a low spring tide. We also calculated “distance to structure” for each string based on an average of the distance to the coastline or artificial structure (e.g. breakwater) of the start and end positions of each string (Supplementary Appendix S4).

We assigned strings of pots to three classes of fishing area based on (i) the district (CIFCA/DSIFCA); (ii) their position relative to the breakwater (landward or seaward); and (iii) the broad-scale fishing area (A–G) in which they were hauled (Figure 1). Fishing areas A–G were defined according to the main fishing areas recorded during the observer surveys and the conditions of wave, wind and current exposure experienced across the Sound, based on their position relative to land, headlands, channels, and the prevailing SSW winds.

For each survey date, we estimated the local average sea temperature between 5- and 10-m depth using linear interpolation of weekly sea temperature data from the Western Channel Observatory’s coastal L4 sampling station, located 10 nautical miles southwest of Plymouth (WCO, 2020; Supplementary Appendix S4). Our choice of covariates is justified in Supplementary Appendix S4.

Data analysis
We used R v3.6.1 or later (R Core Team, 2019) for all data analyses, and QGIS (v3.1) for plotting maps.
Appendix S1 for estimates of overall fishing effort and total number of fishing trips. We used AIC-based model selection to define the most parsimonious GLMs to a maximum of five predictors to avoid overfitting, and standardized to have zero mean and unit variance. We restricted all predictor combinations of predictors and two-way interactions between spatial/environmental and temporal predictors. All possible combinations of predictors and two-way interactions between spatial/environmental and temporal predictors. All continuous predictors (DOY, Dist, Temp, and TR) were standardized to have zero mean and unit variance. We restricted all GLMs to a maximum of five predictors to avoid overfitting, and used AIC-based model selection to define the most parsimonious model from among a candidate set of well-fitting models. See Supplementary Appendix S4 for details of model selection and diagnostic tests, and Supplementary Appendix S6 for all candidate models with ΔAIC ≤ 6. All GLMs used Gamma errors with identity link except for cases in which model diagnostics and fit were improved by use of a log link. Tukey tests with p-values adjusted for multiple comparisons were used to test for significant differences between levels of categorical predictors in the final models.

Results

A total of 133 strings of pots from 29 fishing trips were surveyed across the study period (61, 44, and 28 strings from 12, 10, and 7 fishing trips in 2017, 2018, and 2019 respectively). This represents ~8%, 10%, and 12% of all fishing trips across the July–October period of each survey year, respectively (DSIFCA, unpublished data). A total of 7,089 wrasse (496 ballan, 1,676 corkwing, 3,077 goldsinny, 1,767 rock cook, and 73 cuckoo) were caught, identified and measured across all surveys. See Supplementary Appendix S1 for estimates of overall fishing effort and total numbers of wrasse caught in the fishery each year (from both surveyed and non-surveyed trips).

Year effects

Ballan CPUE and LPUE declined across the survey period but for CPUE this change was only significant between 2017 and 2018 (Table 1 and Figure 2). There was strong support across the candidate models for these year effects on ballan CPUE and LPUE (Supplementary Appendix S6), though LPUE declines were only evident landward of the breakwater (Table 1 and Figure 2). This interaction effect also had moderate support across the candidate models for CPUE (Supplementary Appendix S6), but was absent from the final, most parsimonious model. Ballan wrasse were typically larger seaward of the breakwater than landward (Table 1).

Calculation of CPUE and LPUE

CPUE and LPUE were calculated for each species. CPUE was calculated per string as the number of wrasse caught divided by the number of pots in the string. CPUE includes all wrasse, whether kept or returned to sea, whereas LPUE was calculated as per CPUE, but using the subset of the catch that was landed (wrasse were within the CRS ranges defined by the respective IFCAs: Supplementary Appendix S3, and not damaged or dead). Soak time did not influence catches of any species of wrasse in this system (Supplementary Appendix S5), and is therefore not considered as a component of effort in these analyses.

Statistical modelling

We used generalized linear models (GLMs) to look for evidence that putative predictors (each justified in Supplementary Appendix S4) could explain the variability in wrasse CPUE and LPUE within Plymouth Sound. We considered day of year (DOY), year (Y), fishing district (CD), breakwater position (BW), broad area (BA), average distance to structure (Dist), depth band (DB), bait type (Bait), sea temperature (Temp), and TR as putative predictors. For all species, we considered all plausible combinations of predictors and two-way interactions between spatial/environmental and temporal predictors. All continuous predictors (DOY, Dist, Temp, and TR) were standardized to have zero mean and unit variance. We restricted all GLMs to a maximum of five predictors to avoid overfitting, and used AIC-based model selection to define the most parsimonious model from among a candidate set of well-fitting models. See Supplementary Appendix S4 for details of model selection and diagnostic tests, and Supplementary Appendix S6 for all candidate models with ΔAIC ≤ 6. All GLMs used Gamma errors with identity link except for cases in which model diagnostics and fit were improved by use of a log link. Tukey tests with p-values adjusted for multiple comparisons were used to test for significant differences between levels of categorical predictors in the final models.

Other (exogenous) drivers of change

CPUE and LPUE vary between fishing areas for all species except corkwing (Table 1 and Figure 3). The fishing areas that yield the highest catch and landings are relatively consistent within a species (i.e. across catch and landings), but differ between species (Table 1 and Figure 3).

Discussion

This study identified key drivers of variation in a multispecies inshore fishery, with a view to assessing its sustainability. Using monitoring data from the Inshore Fisheries and Conservation Authorities (IFCAs) in southwest England, and fine-scale environmental data from across the 2017–2019 survey period, we found species-specific responses to environmental, temporal and spatial variables that have implications for future fisheries management.

Year effects

There was evidence of inter-annual declines in ballan wrasse only: CPUE and LPUE declined over the 2017–2019 period, apparently driven by a decrease in abundance of in-size ballan landward of Plymouth breakwater (Figure 2b and Supplementary Appendix S7). A range of evidence suggests that this is likely to be a response to fishing pressure over the study period, though it is not possible to rule out potential confounding effects such as concurrent poor recruitment, increased natural mortality or declines in prey species, which were not studied here. The largest declines in CPUE and LPUE were observed following 2017, the year with the highest fishing pressure (Supplementary Appendix S1). Additionally, the ballan retention rate is generally high in areas landward of the breakwater, which likely interacts with specific life history and behavioural traits (below) that make this species highly vulnerable to fishing pressure, even under the current management measures. Firstly, the closed seasons for the live wrasse fishery in Plymouth Sound (Supplementary Appendix S3) may not protect
Table 1. Parameter estimates (and standard errors) for drivers of variation in catch (C) and landings (L) per unit effort in the selected, most parsimonious model for each wrasse species

|                | CBallan | LBallan | CBookwing | LBookwing | CGoldsinny | LGoldsinny | CRock cook | LRock cook |
|----------------|---------|---------|-----------|-----------|------------|------------|------------|------------|
| \( \beta_0 \)  | -1.834  | -1.666  | 0.373     | -1.322    | 0.858      | 0.231      | -0.928     | -2.027     |
| BA_A           | 0.198   | 0.142   | -0.343    | 0.042     | -0.050     | -0.050     | -0.116     | -0.200     |
| BA_B           | 0.245   | 0.183   | -0.526    | -1.205    | -0.330     | -0.330     | -0.050     | -0.200     |
| BA_C           | 0.587   | 0.160   | 0.370     | -1.074    | 0.630      | 0.630      | 0.392      | 0.392      |
| BA_D           | -0.660  | 0.271   | 0.133     | 0.345     | 0.157      | 0.157      | 0.222      | 0.222      |
| BA_E           | -0.612  | 0.264   | 0.770     | 0.720     | -0.122     | -0.122     | 0.393      | 0.393      |
| BA_F           | 0.056   | 0.171   | -0.293    | 0.528     | 0.214      | 0.214      | -0.146     | -0.146     |
| BW_1           | -1.181  | 0.280   | -         | -         | 0.079      | 0.079      | 0.002      | 0.002      |
| CD_1           | 0.430   | 0.198   |          |          | -          | -          | -          | -          |
| DB_A           | -       | 0.547   | -0.547    |          | -          | -          | -          | -          |
| DB_B           | -       | 0.083   | 0.157     |          | -          | -          | -          | -          |
| DB_C           | -       | 0.078   | 0.115     |          | -          | -          | -          | -          |
| Dist            | -       | -       | 0.217     | 0.035     | 0.245      | 0.103      | -          | -          |
| DOY            | -       | 0.149   | 0.489     | -0.055    | 0.131      | -0.116     | -          | -          |
| Temp            | 0.227   | 0.077   | 0.252     | -0.102    | -          | -          | -          | -          |
| TR             | -       | -       | -         | -0.034    | -          | -          | -          | -          |
| Y2018          | -0.692  | 0.170   | 1.462     | 0.055     | 0.010      | 0.329      | 0.090      | 0.090      |
| Y2019          | -0.416  | 0.188   | 0.605     | 0.378     | 0.101      | -0.832     | 0.090      | 0.090      |
| BW: Y2018      | -       | 0.124   | 0.265     | -0.010    | -          | -          | -          | -          |
| BW: Y2019      | -       | 0.334   | 0.049     | 0.010     | -          | -          | -          | -          |
| Dist: DOY      | -       | -       | 0.217     | -0.102    | -          | -          | -          | -          |

Selected models contain a subset of the fixed effects from: broad area (BA), breakwater position (BW), fishing district (CD), depth band (DB), distance to shore/structure (Dist), day of year (DOY), sea temperature (Temp), tidal range (TR), year (Y), and interaction terms for BW: Y and Dist: DOY. Other interaction terms were tested, but not detected in the final selected models. \( \beta_0 \) denotes the intercept. DB was fitted as an ordered factor with orthogonal polynomial contrasts, so parameter estimates are presented for the linear (DBL), quadratic (DBQ) and cubic (DBC) terms. BA was fitted as zero-sum contrasts, whereas BW, CD, and Y are presented as treatment contrasts.

Figure 2. Predicted effects of year on CPUE (total number of fish per pot) and LPUE (number of landed fish per pot) of ballan (a, b), corkwing (c), and goldsinny wrasse (d) caught in Plymouth Sound between 2017 and 2019, as estimated by GLMs. Error bars represent 95% CIs around the predicted means. Ballan LPUE predictions are split by breakwater position to highlight the interaction effect between these two variables. Coloured points represent raw CPUE and LPUE data per string. *, **, *** denote significant differences (\( p < 0.05, p < 0.01, p < 0.001 \)) in CPUE/LPUE between years (Tukey tests with \( p \)-values adjusted for multiple comparisons).
Figure 3. Predicted effects of spatial variables (broad area and fishing district) on CPUE (total number of fish per pot) and LPUE (number of landed fish per pot) of ballan (a, b), goldsinny (c, d), and rock cook (e, f) wrasse caught in Plymouth Sound between 2017 and 2019 as estimated by GLMs. Error bars represent 95% CIs around the predicted means. Coloured points represent raw CPUE and LPUE data per string. *, **, *** denote significant differences ($p < 0.05$, $p < 0.01$, $p < 0.001$) in CPUE/LPUE between all factor levels except when specific pairwise comparisons are shown with a linking line (Tukey tests with $p$-values adjusted for multiple comparisons). NS denotes no significant difference between specified factor levels.
ballan during their spawning season. This may prevent spawning individuals contributing to recruitment before they are removed from the fishery (Skiftesvik et al., 2014a) and could also reduce the likelihood of egg survival if nest-guarding adult males are removed (Darwall et al., 1992). The timing of ballan spawning can vary by up to several months between locations (Darwall et al., 1992; Muncaster et al., 2010; Villegas-Ríos et al., 2013) and, without a robust assessment of the timing of spawning in southwest England, it is difficult to ensure that spawning individuals and their eggs are protected.

Furthermore, ballan wrasse are protogynous hermaphrodites: individuals develop from females into males after a number of years (Dipper and Pullin, 1979; Muncaster et al., 2013). The length of ballan wrasse at sexual maturity and sexual inversion varies across the species’ distribution, and the length at sexual inversion, which is primarily driven by social cues (i.e. the absence of functional males; Dipper and Pullin, 1979), is plastic within locations. Length at maturity estimates range from 16 to 18 cm for females and around 28 cm for males (Darwall et al., 1992). However, this latter estimate is for individuals that have already undergone sexual inversion; the L50 for ballan (the length at which 50% have undergone inversion) likely lies between 34 and 36 cm, so the size at maturity for most male ballan is likely much higher than 28 cm (Villegas-Ríos et al., 2013; Leclercq et al.,

**Figure 4.** Predicted effects (with shaded 95% confidence intervals) of day of year, distance to structure (m) and sea temperature (°C) on CPUE (total number of fish per pot) and LPUE (number of landed fish per pot) of corkwing (a–c), goldsinny (d–f), and rock cook (g–i) wrasse caught in Plymouth Sound between 2017 and 2019 as estimated by GLMs. Rock cook LPUE predictions for distance to structure are split by day of year to highlight the interaction effect between these two variables. Coloured points represent raw CPUE and LPUE data per string.
2014). Appropriate size restrictions are therefore vital to avoid sex-selective fishing. Under current management measures and fishing patterns, the fishery in Plymouth Sound is likely to be highly selective towards mature female ballan wrasse below the L_{50}, despite the enforcement of narrower CRS ranges than in Norwegian and Swedish fisheries (Rueness et al., 1992). Targeting size classes of protogynous fish below the L_{50} is likely to cause stock crashes at relatively low levels of fishing mortality (or, in this case, live removals; Alonzo and Mangel, 2004); an upward revision of the ballan CRS range should therefore be considered in this area, which already has strict fishing effort controls.

Despite the high retention of corkwing prior to the 2018 CRS changes (Supplementary Appendix S7), corkwing CPUE and LPUE remained stable over 2017–2018. This may be because the 12 cm minimum CRS was above the suggested length at maturity (≈10 cm; Darwall et al., 1992). However, in summer 2018, the corkwing CRS range changed to 14–18 cm and corkwing CPUE increased in 2019. LPUE did not show a similar increase in 2019 (despite a reduction in CRS range), suggesting that the CPUE increase was driven by an increase in the non-landable sizes of corkwing. Yearly size frequency histograms (Supplementary Appendix S7) indicate a recent increase in the smallest size classes, which may suggest recently improved recruitment. The CRS changes may have increased the proportion of mature males (which tend to be larger; Halvorsen et al. 2016) that were being returned to sea, and afforded protection to large and more fecund individuals of both sexes, aiding recruitment (Birkeland and Dayton, 2005; Kindsvater et al., 2020). Goldsinny LPUE was lowest in 2018, following the year of most intense fishing effort (Supplementary Appendix S1). However, unlike in ballan wrasse, goldsinny LPUE recovered in 2019, perhaps because the CRS range applied allows a large enough proportion of mature individuals to be returned to the sea (Supplementary Appendix S7; Darwall et al., 1992); at lower fishing effort levels, this CRS range may be sufficient to allow stock recovery.

Other drivers of variation in catch and landings

We identified exogenous drivers of variation in wrasse catches and landings that, in many cases, reflect species-specific patterns that have been identified in wrasse from other regions. For example, corkwing LPUE was higher in shallower areas of in Plymouth Sound, which supports the shallow water preferences observed in Norway and the northeast Atlantic (Quinard and Pras, 1984; Skiftesvik et al., 2014a,b). Halvorsen et al. (2020) found variation in depth for catches of other wrasse species that was not observed in this study; this difference may have arisen as Halvorsen et al. (2020) were able to survey catches over a wider range of depths, measured using depth loggers rather than coarser-resolution depth bands derived from remotely sensed bathymetry data.

Goldsinny CPUE and LPUE were lower in areas closest to the freshwater input from the River Tamar (broad areas A and B), which corroborates previous observations of lower goldsinny densities at sites influenced by freshwater runoff (Sayer et al., 1993), and further highlights our ability to detect fine scale species-specific drivers of relative abundance. Additionally, rock cook CPUE was lower in the more sheltered areas (broad areas B and C) and nearer to shore or man-made structures; this supports earlier observations of lower rock cook abundance in more sheltered locations in Norway (Skiftesvik et al., 2014b). Survey effort was uneven across years between exposed and sheltered locations (Figure 1): considerably more strings were surveyed in exposed areas in 2017 (62 strings) than in 2019 (12 strings), and vice versa for the sheltered areas (8 strings in 2017, 23 strings in 2019). By accounting for fishing location in our analyses, we reduced the risk of identifying a false year effect for rock cook that might have resulted from uneven survey effort across locations, and environmental preferences of target species. Conversely, Curtin et al. (2020) reported a significant decline in rock cook CPUE and LPUE in DSIFCA waters of Plymouth Sound over the 2017–2019 period. Unlike this study, Curtin et al. (2020) could not account for other exogenous drivers of change and, importantly, used data from differing time periods within each year. CPUE and LPUE of rock cook (and other species) vary with day of year, so inter-annual comparisons must consider equivalent time periods.

Corkwing CPUE and LPUE increased with day of year, from July to October, perhaps partly reflecting their changing intra-annual activity levels (and hence differing levels of catchability). For example, nesting male corkwing wrasse exhibit high site fidelity for nest guarding during the spawning season (thought to end by early August in this location; Potts, 1974; Darwall et al., 1992; Halvorsen et al., 2016). Halvorsen et al. (2017) found that nesting males showed higher catchability than females during the spawning season, but did not investigate variation in catchability over the fishing season. Closer investigation is required to identify drivers of the seasonal variation identified here.

Little is known about rock cook spawning or seasonality in activity and distribution. Here, rock cook catches showed similar seasonal (day of year) variations to corkwing, and a similar variation with distance to structure to goldsinny. However, the relationship between rock cook landings and distance to structure changed from positive to negative as the fishing season progressed: landings reduced over the season only in areas furthest from shore or man-made structures. This might suggest that rock cook further from shore is being removed unsustainably, but have a chance to recover between fishing seasons (typically January–June inclusive). However, it should be noted that the sample size is relatively low further from shore, and inconsistencies in temporal distribution of survey effort between years restricted our analyses to the July–October period. Within the time- and resource-limited research capabilities of the regional ICAs, future surveys should aim to distribute survey effort evenly and consistently over time and locations, accounting for the important drivers of CPUE and LPUE identified here, to achieve robust monitoring and recommendations for management.

Finally, sea temperature has previously been highlighted as a driver of wrasse activity and catches (Darwall et al., 1992; Sayer et al., 1993; Gjosaeter, 2002), explaining up to half of the catch rate variation for all species in western Norway (Thangstad, 1999). However, in this study, only corkwing landings were influenced by sea temperature, and with a relatively small effect size. The lowest sea temperature recorded during our study was 14.5°C, which is ≈7°C warmer than typical temperatures in Plymouth Sound during the coldest months (March–April; WCO, 2020). During winter in Norway and Scotland, sea temperatures can drop to 5°C at 4- to 6-m depth; changes in wrasse behaviour and physiology allow them to survive these conditions, and also reduce catch rates (Sayer et al., 1994; Sayer and Davenport, 1996; Sayer and Reader, 1996). The overall lack of temperature effects may reflect the generally warmer sea temperatures experienced in southwest England compared with Norway,
and the shorter survey period that did not include the coldest months. This re-emphasizes the importance of distributing survey effort consistently and evenly over time and space in the future, so we are better able to capture location-specific seasonal variations in wrasse abundance and assess their implications for fisheries management. On-board sea temperature measurements should also be considered in future survey design to increase the accuracy of temperature data.

Conclusions
Our study provides the first robust analysis of the effects of the multispecies wrasse fishery in southwest England. We assess the main drivers of variation in wrasse catches and landings, and the suitability of current management measures in delivering sustainability. Wrasse are harvested for use in salmon aquaculture from many locations regionally (Dorset and further west in Cornwall), nationally (Scotland and Ireland), and internationally (Norway). In many cases the local fishery is much larger than that in Plymouth Sound, both in terms of landings and geographic extent (Riley et al., 2017; Norwegian Directorate of Fisheries, 2020), but there is limited systematic monitoring to inform management. Our study demonstrates the insight that can be gained from fisheries-dependent surveys with relatively little observer effort, and supports a need for adaptive local management, in this case via local byelaws, to allow landings of rock cook (previously prohibited), and to revise the ballan CRS range to better protect mature females. Management measures in other live wrasse fisheries have been or are being developed based on the example set by the IFCA in southern England. Therefore, our methods and findings are likely to have wider ramifications across all wrasse fisheries, which would benefit from similar low-effort monitoring approaches to enable adaptive management. Alternative monitoring and management approaches are possible, such as harvest control rules that account for variation in recruitment, mortality, growth, and other life-history parameters. However, these require detailed data that may take many years and substantial investment to collect; we show that, in data-poor fisheries such as this, interim approaches applied to fisheries-dependent survey data provide robust insights for appropriate management.

We have shown that these mesopredatory species respond differently to fishing pressure and eco-geographical variables, confirming the importance of considering the different species separately for management purposes. The current extensive management measures have largely been based on evidence collected in other locations (particularly Norway), but appear to be insufficient to safeguard local populations of ballan wrasse in particular. Clearly, care must be taken in basing management decisions on evidence from populations in distant locations (Halvorsen et al., 2016). The management of live wrasse fisheries would therefore benefit from location-specific assessments of spawning season, size at maturity and L50. These measures should be monitored as the fisheries progress, to inform management and provide a better understanding of the full extent of plasticity and variability of sex change in this hermaphroditic mesopredator.

In highlighting the main drivers of variation in catch and landings between wrasse species, we particularly showed the importance of including fishing location as a variable. Wrasse catches and landings varied significantly over small spatial scales, likely due to differing habitat types or conditions experienced in the areas (e.g. exposure, freshwater influence). If these environmental variables are not accounted for throughout survey design and data analyses, incorrect conclusions may be drawn regarding fishery effects and sustainability, as appears to have happened previously for ballan and rock cook (e.g. Curtin et al., 2020).

Finally, wrasse play an important role as predators (of molluscs, crustaceans, and echinoderms; Deady and Fives, 1995; Sayer et al., 1995, 1996a), prey (e.g. for otters, seabirds and commercially important gadoids; Steven, 1933; Pinney, 2011) and as cleanerfish (Henriques and Almada, 1997; Galeote and Otero, 1998; Morado et al., 2019). Therefore, ecological consequences for predator, prey, and client species may be anticipated if fisheries modify wrasse abundance and/or assemblage composition; the role of wrasse within these ecosystems is therefore a priority for future research.

Supplementary data
Supplementary material is available at the ICESJMS online version of the manuscript.

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Authors’ contributions
L.H. and S.D.S. conceived the ideas, L.H. and J.E.S. designed the methodology and obtained the data; L.H. analysed the data and led the writing of the article. All authors contributed critically to the drafts and gave final approval for publication.

Data availability
Data are available at https://doi.org/10.24378/exe.3243.

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