

MODEL-BASED SAMPLING DESIGN FOR EASTERN BLUEFIN TUNA CLOSE-KIN MARK RECAPTURE

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SUMMARY

This report develops a spatially-explicit Close-Kin Mark-Recapture (CKMR) model suitable for Eastern Bluefin Tuna (BFT-E) and uses it to investigate some sampling options (e.g., sample sizes by fishery, number of years, whether to preferentially subsample bigger or smaller fish, etc) to check what kind of precision might be achievable for quantities of interest (mainly, total abundance of adult BFT-E) and by when.

RÉSUMÉ

Ce rapport développe un modèle de marquage-recapture de spécimens étroitement apparentés (CKMR) spatialement explicite, adapté au thon rouge de l'Est (BFT-E), et l'utilise pour étudier certaines options d'échantillonnage (par ex. les tailles d'échantillons par pêcherie, le nombre d'années, déterminer s'il est préférable de sous-échantillonner des plus grands poissons ou des poissons plus petits, etc.) afin de vérifier le type de précision qui pourrait être obtenue pour les quantités d'intérêt (principalement l'abondance totale de thon rouge de l'Est adulte) et dans quel délai.

RESUMEN

En este informe se desarrolla un modelo de marcado y recaptura de individuos estrechamente emparentados (CKMR) espacialmente explícito adecuado para el atún rojo del este (BFT-E) y se utiliza para investigar algunas opciones de muestreo (p. ej., tamaños de muestra por pesquería, número de años, si se deben realizar submuestras preferentemente de peces más grandes o más pequeños, etc.) para comprobar qué tipo de precisión podría alcanzarse para las cantidades de interés (principalmente, abundancia total de BFT-E adultos) y para cuándo.

KEYWORDS

Close-Kin Mark-Recapture (CKMR), design, abundance estimation, bluefin tuna

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1. Introduction

This report develops a spatially-explicit Close-Kin Mark-Recapture (CKMR) model suitable for Eastern Bluefin Tuna (BFT-E), and uses it to investigate some sampling options (e.g., sample sizes by fishery³, number of years, whether to preferentially subsample bigger or smaller fish, etc), to check what kind of precision might be achievable for quantities-of-interest (mainly, total abundance of adult BFT-E) and by when.

It is fairly easy to use the model to investigate other proposed sampling schemes, but the first step would be to discuss logistic issues and objectives in more detail, starting at the Malta intersessional workshop in mid-April; further investigations could be done in follow-up work over the next few months (i.e. for July). The model developed here is deliberately simplified, as discussed below, but once a full-scale CKMR project is underway, it could form the basis of a fully-realistic model for analysing the real data, especially in respect of the spatial aspects; some other aspects of the model would need further development, as described later.

This report addresses the 4 Tasks identified in Call for Tenders: ICCAT GBYP 01/2024: *Model-based sampling design for eastern bluefin tuna close-kin mark recapture Atlantic-wide Research Programme for Bluefin Tuna*. Those tasks are:

1. Develop a population dynamics model for the three main Mediterranean Sea spawning groups (subpopulations), that can represent alternative hypotheses about site fidelity, stock mixing within the Mediterranean and in the Atlantic, and differential fishing mortality among subpopulations;
2. Specify probabilities of POPs and HSPs, conditional on each of the specific hypotheses outlined under item 1;
3. Use the spatial model as an operating model to evaluate the performance of alternative multi-year sampling schemes for POPs and HSPs, suggesting options for the type and number of samples to be collected from different geographic areas/fisheries;
4. Use the spatial model to explore how the data might reveal departures from baseline hypotheses made for item 3; for example, that two or three of the subpopulations are fully mixed in the Atlantic, and that there is spawning site fidelity.

Several previous ICCAT/GBYP-funded studies have considered various aspects of BFT-E CKMR in broad terms (e.g. Davies *et al.* 2017; Anon 2021; Anon 2023). However, this is the first one to develop a quantitative CKMR model that explicitly addresses spatial structure, and the first one where there is a clearly-defined set of fisheries to consider. The 2017 report did some quantitative investigation, but it was not spatially-structured, and expertise in CKMR is much more advanced now than it was in 2017, when only one or two species (primarily Southern Bluefin Tuna, SBT) had been studied.

Notwithstanding the specific Tasks above, the general aim of CKMR Design is to minimize the risk of setting up a project that is doomed to fail. From a Design perspective, the key things to avoid are:

- too few samples to get any useful precision;
- bad balance of samples (e.g. fish sizes, years covered, places sampled);
- inadequate measurement of covariates, especially size and/or age.

In this report we deal only with the first two aspects (but see Discussion section, at the end of this report, for some comments on the third). Of course, there are other critically-important things that need careful attention to avoid a CKMR project going wrong (e.g. logistics of tissue collection, and genotyping), but those are rather separate from Design aspects we consider here.

Definitions of subpopulations and fisheries

Based on the 2023 ICCAT Workshop on CKMR (Anon 2023) and on follow-up interaction with other scientists, we assume there are three main spawning grounds within the Mediterranean Sea (West, Central, East/Elsewhere, denoted by W , C and E in the sequel) with individual tuna possibly showing a persistent preference for one specific ground, or possibly not showing this type of behaviour. The subset of BFT-E adults using each ground in any year (a subset which is not necessarily persistent across years) is called a subpopulation. Note that fisheries in the Atlantic may catch a mix of BFT-E and BFT-W (spawning in Gulf of Mexico, etc), with the latter forming a

³ Our fisheries also include the Balearic larval survey, which is obviously not a fishery. However, it is simpler to just use the one word “fishery” to describe all sources of samples, as well as (depending on the context) actual fisheries that cause removals from the populations.

biologically separate population; previous recent work has shown that BFT-W and BFT-E can be distinguished genetically with good confidence, so we simply assume that any BFT-W samples will be eliminated before any kinship comparisons between BFT-E animals are undertaken. Samples from the Mediterranean and the Straits of Gibraltar area are entirely BFT-E for all practical purposes. To avoid confusion, we always use the term BFT-W for animals from the Western Atlantic population, whereas *W* on its own refers to the West Med spawning ground and/or subpopulation.

Again based on the 2023 ICCAT Workshop on CKMR, we have considered five fisheries as potential sample sources: Balearic larvae (technically not a fishery), Croatian juveniles, *W* adults, *C* adults, and Atlantic adults. Details of age ranges, etc are given in the main sections of this report, but a few general notes on each of them are included here. A key point for each fishery is how mixed it is (i.e. what its "mixity" is): a well-mixed fishery is one where catches are taken in proportion to the abundance of each Med subpopulation; a pure fishery comprises catches from one known subpopulation only; and a partly-mixed fishery (i.e. one with intermediate mixity) has a mix in unknown proportions of animals from at least two subpopulations.

Balearic larvae

Denoted as *Wlar* in the sequel.

These are fish of known age from the *W* subpopulation, that can be collected in large quantities (many thousands per year), and samples are archived back to 2019.

One problem with larval samples is that intra-cohort sibship might be high, because half- and full-siblings from the same spawning event may still be schooling together when they are caught. The problem this causes is that kinship comparisons to other samples in other years and places are no longer statistically independent, not even approximately; if one Balearic larval sample finds its mother, then that increases the chance that other Balearic samples from that year will also find their mother, because some are likely to have the same mother and we know she (the mother) has been sampled. Although this does not technically cause bias, it can substantially reduce the statistical information content of each larva; i.e., overall precision is substantially lower than it would be if the same number of samples were taken from a non-larval fishery. The issue is non-ignorable for BFT-W larval samples, and the effective sample size may only be about 50% of the actual sample size. Intra-cohort sibship certainly occurs within Balearic samples, as documented in previous ICCAT reports, although not at disastrous levels based on the 477 samples from 2018 examined so far⁴. However, the extent is quite nonlinear in sample size (it gets worse the bigger the sample), and the impact for a full annual sample of say 5000 individuals cannot be predicted; to find out, an entire year's sample should be genotyped.

Ultimately, the presence of substantial intra-cohort sibship among samples can necessitate a structural change to CKMR probabilities, well beyond the calculations shown in this report. The mathematics have been developed for BFT-W but implementation is still in progress. Since Balearic samples are likely crucial for BFT-E CKMR analysis, something similar will ultimately be needed, but it is impossible to incorporate it into design calculations. For now, we have made an ad-hoc adjustment of 0.5 to the larval sample sizes (similar to the worst year in the BFT-W study) to perform the CKMR calculations for the results shown under Tasks 3 and 4, although the sample sizes shown in the report are actual numbers sampled (i.e. before applying the adjustment), since the actual numbers sampled directly reflect cost and logistics.

Croatia juveniles

Denoted as *CROjuv* in the sequel.

These are likely to be partly-mixed fish from the three subpopulations; in any case, we cannot safely assume that they are e.g. pure *C*-origin fish, and the mixing proportions are unknown. It nevertheless provides a useful second source of juveniles that are not all *W*-origin and, in conjunction with the other fisheries, *CROjuv* samples should let us deduce a great deal of information about spatial structure within the Med subpopulations (see Appendix). Since the fishery takes some age-4 animals, it also extends the CKMR study back in time (although the archived Balearic larvae go back even further, to 2019). Age data will likely be essential for these fish, since length does not seem particularly reliable at distinguishing age classes for BFT-E, even at such young ages. One important aspect of CKMR studies is the span of birth-cohorts with reasonable numbers of samples; it may be worth over-sampling large compared to small fish in the *CROjuv* fishery, at least at the start of the project, in order to stretch the study further back in time.

⁴ See e.g. background presentation to 2021 ICCAT GBYP Workshop on CKMR for BFT-E (Feb 2021)

W adults and C adults

Denoted as *Wad* and *Cad*, respectively, in the sequel.

Wad are fish caught on the *W* spawning ground and are pure *W* samples (i.e. from the *W* subpopulation in the year the sample is taken). A similar situation occurs with *Cad* fish relative to the *C* spawning ground. Qualitatively, these two pure samples, in conjunction with all others, provide information on within-Med spatial structure, e.g. on persistence of the subpopulations and, if there is persistence, on the split of abundance between the subpopulations.

These samples will be used mainly as potential parents, but also as potential offspring, in CKMR comparisons.

Atlantic adults

Denoted as *ATLad* in the sequel.

There are at least three Atlantic fisheries which can provide substantial numbers of BFT-E samples: Portuguese traps, Canada, and Norway. It is a reasonable working assumption, consistent with satellite tagging results, that almost all big BFT-E move into the Atlantic to feed, and thus that the Atlantic fisheries are well-mixed with respect to Med subpopulations (at least with respect to *W* and *C* subpopulations). This makes the Atlantic samples ideal for estimating aggregate BFT-E abundance, when compared against either Balearic larvae or Croatian juveniles (or both).

Since all the samples from Atlantic fisheries are expected to behave in the same way from a CKMR perspective, for this report we have treated all Atlantic fisheries as a single pool. However, in Task 4 (and more explicitly in the Discussion section) we consider the possibility of checking that assumption as CKMR data accumulate.

These samples will be used mainly as potential parents, but also as potential offspring, in CKMR comparisons.

Complications and simplifications

Before going into details of the model, it is worth emphasizing that BFT-E CKMR is, by some margin, the most complicated CKMR application yet considered⁵, because of the potential for spatial structure that could make things go badly. There is no pre-existing spatial framework, and all the equations and computer code for BFT-E had to be developed from scratch, within a short timeframe. To get something ready in time, it has been necessary to simplify some aspects (relative to what might be included in a model for real data analysis), as well as to limit both the number of *scenarios* considered (i.e., different assumptions about true abundance and true spatial structure) and the range of sampling schemes investigated (i.e., different possible sample sizes, etc).

With the model itself, our aim has been to develop a model and its data specifications that have roughly the same degree of difficulty in parameter estimation as a real model would have, while simplifying the details as much as possible. Two main examples of simplifications are that the model developed is completely age-based, rather than length-and-age based, and that a separable-*F* (fishing mortality) model with the selectivities treated as inputs has been assumed, rather than a model which explicitly incorporates catch at size. If a CKMR project gets underway, these model aspects will have to be addressed in time for the statistical analysis of the observed CKMR data.

Structure of the document

The rest of this report follows the four Tasks indicated above (Sections 2 to 5), followed by Discussion (Section 6) and Conclusions (Section 7). Although we calculate likely coefficients of variation (CV) under two possible sampling schemes, these should not be interpreted as definite proposals; rather, they are a starting point for discussion. The sample sizes we include are based on general discussions with fishery experts of what might be achievable; we wanted to see if such sample sizes would likely lead to good precision within a reasonable timeframe (spoiler: yes they should; and some rather vague but still useful results might be obtained even by 2027, if things move quickly). However, we have not attempted to optimize the sampling scheme (although we did investigate a couple of alternatives, partly just to demonstrate that it can be done easily), since optimization would need to involve at least:

- some agreement on target CVs;
- comparative logistic issues amongst different fisheries;

⁵ BFT-W has been complicated too, but for a completely different reason: the reliance on larval samples where intra-cohort sibship is high. The mathematical methods that now have been developed to deal with that for BFT-W will be directly useful for BFT-E too, in dealing with the Balearic larval samples. In comparison to those, CKMR for Southern Bluefin Tuna was almost simple. In the other 8–10 applications of CKMR, e.g. to School Shark and to conservation species such as Fruit Bats, the main complication has tended to be poor-quality measurements of age and/or size— something which hopefully is not going to plague BFT-E.

- estimates of intra-cohort sibship within an entire single-year Balearic sample;
- information on epigenetic ageing costs.

CKMR Design is critically important in order to avoid the big mistake of spending a lot of money but not enough to get a useful result, when that outcome could have been predicted in advance. However, because the optimal design depends on many variables (in particular on the abundance, which is unknown), it is more realistic to think about initial Design as a way to make sure that CKMR gets off to a clearly-useful start. The design itself, i.e. sample sizes, sample breakdown, number of years required, may well need adjustment (and even optimization) in the light of information acquired during the first few years.

For the calculations shown under Tasks 3 and 4 in this report, we have made some working assumptions about abundance and spatial structure, added some notional sample sizes, as just discussed, over the years 2025–2030 (actually 2019–2030, with the inclusion of Balearic archive samples), and explored:

- what *quantitative* precision we might expect for various parameters (abundance and mortality), if the working assumptions are approximately right; and
- what *qualitative* level of statistical power we might have to detect whether those assumptions (particularly the spatial ones) are in fact reasonable;

We mainly consider what might be learnt by sampling up to 2030, but also how much information we might be able to get by 2027.

2. Population Dynamics Model

In this section, we address Task 1: “Develop a population dynamics model for the three main Mediterranean Sea spawning groups (subpopulations), that can represent alternative hypotheses about site fidelity, stock mixing within the Mediterranean and in the Atlantic, and differential fishing mortality among subpopulations.”

To address this task, we develop an age & sex structured Population Dynamics Model (PDM), with yearly time step, that represents the three main Mediterranean Sea subpopulations/spawning groups (Western, Central and Eastern Mediterranean, denoted by “ground” $r = W, C, E$ in the PDM). Each adult fish is “registered” each year into one of the three subpopulations, but may change its registration in the next year.

The PDM is described in this section:

- $N(s, y, a, r)$ = population numbers of sex s (F, M) and age a in year y , registered at ground r (W, C, E) in year y .
- The model starts at age $A_{min}=2$ (when fish may first appear in a fishery, which is the Croatian juvenile fishery) and go to a plus age group, A_{max} (30+, as in the 2022 SS3 BFT-E assessment).
- The year range considered in this model, which has been specifically developed for the CKMR design purpose, is from Y_{min} to Y_{max} , initially taken as the year range 2014-2030.
- A fish born at a ground r , is registered at that ground until the age when it first matures; at that point, its registration becomes the ground in which it spawns.

The following model is used for this registration process, which is assumed to occur annually:

- In the first year a fish matures, with probability $pf1$ (where $0 \leq pf1 \leq 1$), the fish does not change ground (i.e. it spawns in its ground of birth), whereas with probability $1 - pf1$, it *may* change ground; in the latter case, the fish randomly registers at one of the three grounds (W, C, E), with some probabilities $g(r) > 0$ such that $\sum_{r=W,C,E} g(r) = 1$.
- The process just described occurs annually in all subsequent years, with the only difference that a parameter (pf , where $0 \leq pf \leq 1$) is used instead of $pf1$.

The values of $pf1$ and pf may be linked to alternative hypotheses about site fidelity to the main spawning grounds, as follows:

- *Heritability* corresponds to $pf1 \approx 1$, i.e. the fish would always choose their ground of birth in the first year in which they spawn.

- *Faithfulness* corresponds to $pf \approx 1$, i.e. after an initial choice of spawning ground (i.e. in the first year in which they spawn), the fish would keep that ground in all subsequent years. This implies that the fish would always spawn on the same ground, although it is not necessarily their ground of birth.
- If *heritability and faithfulness* both occurred (i.e. $pf_1 \approx pf \approx 1$), there would be 3 separate biological populations, one per ground, although the fish from different populations would be caught together in the Atlantic fisheries and possibly in some fisheries in the Med.
- If $pf < 1$, i.e. not faithfulness, the fish could change ground every year throughout their adult life and, therefore, a fish would most likely not spawn always on the same ground. This leads to higher degrees of mixing between the fish from the 3 grounds. The closer the value of pf is to 1, the more likely the fish are to remain registered in the same ground in consecutive years (“stickiness”). At the other extreme, $pf = 0$ implies a complete lack of memory, i.e. the fish would choose a ground each year independently of where they were in the previous year.

The population abundance, $N(s, y, a, r)$, evolves over time as follows:

Recruitment (age 2)

For all years y , $N(s, y, 2, r) = 0.5 Rmed(r) Rdev(y, r)$, where

- $Rmed(r)$ are ground-specific parameters, giving the overall median recruitment per ground,
- $Rdev(y, r)$ are log-Normal recruitment deviations, i.e. $\log(Rdev(y, r)) \sim N(0, sd = \sigma_R)$.

At the recruitment age all fish are immature, i.e. $N_{imm}(s, y, 2, r) = N(s, y, 2, r)$ and $N_{mat}(s, y, 2, r) = 0$, where N_{imm} and N_{mat} denote numbers of immature and mature fish, respectively.

Ages older than 2

For the initial model year ($y = Ymin$), the abundance at each age, $N(s, Ymin, a, r)$, is derived from the abundance at the previous age using a common slope parameter; log-Normal random deviations are subsequently incorporated for each age. In this way, population abundance at age in the first year reflects the combined effect of different recruitment strengths and fishing mortalities in previous years.

The numbers at age in the initial model year, $N(s, Ymin, a, r)$, are split into numbers immature and mature applying the maturity ogive by age and sex, $mat(s, a)$, resulting in:

- $N_{imm}(s, Ymin, a, r) = N(s, Ymin, a, r) \{1 - mat(s, a)\}$
- $N_{mat}(s, Ymin, a, r) = N(s, Ymin, a, r) mat(s, a)$

For subsequent years, $y > Ymin$, the population dynamics processes considered in the model are survival, age incrementation, maturity and registration to a ground, as described below.

The immature fish do not change registration ground. Therefore, for each ground r :

$$N_{imm}(s, y, a, r) = N_{imm}(s, y - 1, a - 1, r) \exp\{-Z(s, y - 1, a - 1, r)\} \frac{1 - mat(s, a)}{1 - mat(s, a - 1)}$$

Clearly, $N_{imm}(s, y, a, r) = 0$ for all ages such that $mat(s, a) = 1$.

The mature fish may change registration ground. From the registration process described above, the following equation is obtained:

$$N_{mat}(s, y, a, r) = \sum_{r'=W,C,E} N_{mat}(s, y - 1, a - 1, r') \exp\{-Z(s, y - 1, a - 1, r')\} pReg(r', r) + \sum_{r'=W,C,E} N_{imm}(s, y - 1, a - 1, r') \exp\{-Z(s, y - 1, a - 1, r')\} \frac{mat(s, a) - mat(s, a - 1)}{1 - mat(s, a - 1)} pReg1(r', r)$$

where the second term in the sum only applies to the ages a such that $mat(s, a - 1) < 1$, i.e. if there is still some immature fish at the age of $a - 1$. In this expression, the factors $pReg(r', r)$ and $pReg1(r', r)$ represent the registration process described above:

$$pReg(r', r) = pf I[r = r'] + (1 - pf) g(r) \quad \text{and} \quad pReg1(r', r) = pf1 I[r = r'] + (1 - pf1) g(r),$$

where $I[r = r']$ is equal to 1 if $r = r'$ and is 0 otherwise.

The last age in the population model (A_{max}) acts as an accumulator age (i.e. a plus group age) and all fish at that age are assumed to be mature.

For each sex, year, age and ground, the total population abundance is the sum of the mature and the immature fish:

$$N(s, y, a, r) = N_{imm}(s, y, a, r) + N_{mat}(s, y, a, r)$$

Mortality $Z(s, y, a, r)$

For possible suggestions on fishing mortality and selectivity from different fishing fleets, the 2022 SS3 BFT-E assessment (Anon. 2022) was considered, as it is fleet-structured and can therefore provide some insights on this. According to that assessment, the biggest sources of fishing mortality in the most recent years are (**Figure 1**):

- Fleet 11: PS-MED (SP+FR, so, presumably, it takes place in the W Med),
- Fleet 12: PS-OTH (rest of countries, so, presumably, it takes place in the $C + E$ Med),
- Fleet 8: PS-HRV (Croatia-juvenile),
- Fleet 14: Traps of SP+PT+MA
- Fleet 5: LL from Japan in the Northeast Atlantic
- Fleet 6: LL-OTH (all LL that is not from the Japanese fleet...maybe in Atlantic and perhaps also in Med),
- Fleet 16: OTH (maybe in Atlantic and Med?)

The resulting fishing mortalities adding up together all the fleets that are not purse-seine are shown in **Figure 2**.

The overall selectivity (Sel_{tot} , in **Figure 3**), taking the relative F_s of the different fleets into account, is estimated to have been very similar in each of the years 2014-2020, suggesting that the proportion of F exercised by the different fleets has probably been fairly constant through this period.

It must be noted that the population dynamics model in the 2022 SS3 BFT-E assessment is not spatially structured and, therefore, the fishing mortalities and selectivities depicted in **Figures 1** and **2**, and Sel_{tot} in **Figure 3**, are relative to the whole BFT-E.

Tuna are mobile fish that can move around and be caught in different Mediterranean and Atlantic fisheries through the year. If we assume the fish from purse-seine fisheries in the Mediterranean Sea are likely to affect more strongly the fish registered at the closest ground to the fishery, whereas all other fisheries affect all fish equally, the overall fishery selectivity may be a bit different for fish registered at different grounds. For example, assuming that Fleet 8 (Croatia juvenile fishery) is four times as likely to affect a fish registered at the C ground compared to a fish registered at the W ground or to a fish registered at the E ground, that Fleet 11 affects only the fish registered at the W ground and that Fleet 12 affects only the fish registered at the C or E grounds, and that it affects the fish at these two grounds equally, we may get selectivities as depicted in **Figure 3** for the fish registered at different grounds, which would be compatible with the overall selectivity estimated by the 2022 SS3 BFT-E assessment (which is Sel_{tot} in the same figure). The figure also suggests that differences in selectivity for ages 5 and older (which are the ages about which CKMR can be most informative) are not likely to be large.

In the PDM developed for CKMR design purposes, we have assumed:

$$Z(s, y, a, r) = M(a) + F(s) \times F(y) \times Sel(a, r) \times F(r),$$

where, for each registration ground r , $Sel(a, r)$ has a maximum value of 1 over the ages. The ground-specific factors, $F(r)$, were treated as unknown parameters, whereas all other parameters were treated as known, as follows:

- The values of natural mortality, $M(a)$, were taken from the 2022 SS3 BFT-E assessment.
- The sex-specific factor $F(s)$ was assumed to be =1 for both sexes.

- $Sel(a, r)$, for each of the 3 grounds was assumed as depicted in **Figure 3**.
- Based on the results of the 2022 SS3 BFT-E assessment and the MSE approved for BFT-E, $F(y)$ (apical F) was assumed to be = 0.07 in 2014 and increasing gradually to a value of 0.15 by year 2023. For subsequent years, it was assumed to remain at the 2023 value.

Fecundity $Fec(s, a)$ and Total Reproductive Output $TRO(s, y, r)$

Fecundity and Total Reproductive Output are relevant for the CKMR probabilities that will be derived in the next section.

We assume: $Fec(s, a) = weight(s, a)^{\gamma(s)}$, where the exponent $\gamma(s)$ is a sex-specific parameter ≥ 0 .

Total Reproductive Output (TRO) at a ground r (W, C, E) is defined as:

$$TRO(s, y, r) = \sum_a N_{mat}(s, y, a, r) Fec(s, a)$$

If the exponent $\gamma(s)$ in the definition of fecundity is equal to 1, then TRO is equivalent to the SSB (spawning stock biomass), whereas if $\gamma(s)$ is bigger than 1, then heavier fish are relatively more fecund (i.e. more fecund per unit of biomass) than lighter fish.

TRO is crucial for calculating CKMR probabilities, but also it is arguably the most relevant statistic for long-term management. Maintaining the population's reproductive potential above "dangerously low values" is the core sustainability requirement of fisheries management, and TRO is by definition a better measure of reproductive potential than SSB . Unlike SSB , though, the units in which TRO is expressed are a matter of choice, because every $Fec(s, a)$ value could be multiplied by some constant without changing the CKMR probabilities at all (see CKMR equations Section 3). A good option with a biologically meaningful interpretation is to choose some reference age, say X , at which the fish are fully mature and which is close to the age-class that collectively contributes the most to overall reproductive output, and then work with the above formula for TRO divided by $Fec(s, X)$. The result is the number of fish of that age X that would have the same TRO as the actual population. This approach is followed for SBTuna, for example, with a reference age of 16.

Mixing of fish from different grounds in the fisheries sampled for CKMR

As already noted, the 3 “grounds” ($r = W, C, E$) in the PDM essentially represent the spawning behaviour of the fish, but the fish move through the year, both within the Mediterranean Sea and going to and/or returning from the Atlantic. The fish may, therefore, be caught in different fisheries through the year, which will affect CKMR probabilities involving individuals sampled from the fisheries.

The following concept will be relevant when deriving CKMR probabilities:

For a fishery f , $\alpha f(a, r)$ denotes the “mixity” of fish of age a in that fishery, i.e. the odds among the 3 grounds ($r = W, C, E$) of a fish appearing in that fishery if that fish is registered at a ground versus if it is registered at another ground.

- If f is a *well-mixed fishery* for fish of age a , then $\alpha f(a, r)$ has the same value for all grounds r (W, C, E), i.e. in any given year, a fish of age a is equally likely to end up in that fishery regardless of the ground at which it is registered.

Therefore, in a well-mixed fishery (for fish of a given age), the proportion of fish from different registration grounds found in the fishery in a given year represents (for that age) the actual proportion in the population in that year.

- Atlantic fisheries are expected to be *well-mixed*, at least for sufficiently big (i.e. old) fish.
- Fisheries in the Mediterranean Sea are expected to be not well-mixed, i.e. a fish may have different probabilities of appearing in a given fishery depending on the ground in which the fish is registered.
- If f is a *pure fishery* on a ground r^* , the fishery only acts on the fish registered at that ground, i.e. $\alpha f(a, r) = I[r = r^*]$.

Parameters treated as unknown (i.e. estimated) and fixed (i.e. not estimated) in the CKMR analysis

Table 1 lists the quantities that were treated as unknown parameters (i.e. those that would be estimated from the CKMR data, using Poisson likelihoods for the number of kin pairs found, based on the probabilities for finding a kin pair in a given comparison derived in Section 3). For the parameters estimated in the CKMR analysis, the values in the column “Initial guess” have been used for the main design work presented in Section 4.

One main aim of a CKMR analysis for BFT-E would be to estimate adult population abundance in absolute terms. The initial guesses made for the values of parameters and other variables, result in the following annual SSB values by year (summing over the 2 sexes and the 3 grounds) shown in **Table 2**.

3. POP and HSP probabilities

In this section we address Task 2: “Specify probabilities of POPs and HSPs, conditional on each of the specific hypotheses outlined under item 1.”

The following expressions will be used many times, in various ways, in the CKMR probability formulae:

- $SurvRegM(s, a, y_0, r_0, y_1, r_1)$, defined as the probability that a fish of sex s and age a in year y_0 which is mature in that year and registered at ground r_0 in that year, subsequently survives to year y_1 and is registered at ground r_1 in that year.

$SurvRegM(s, a, y_0, r_0, y_1, r_1)$ can be calculated recursively, going forwards in time year by year, as follows:

For any $r_1 = W, C, E$, we have:

$$SurvRegM(s, a, y_0, r_0, y_0 + 1, r_1) = \exp\{-Z(s, y_0, a, r_0)\} pReg(r_0, r_1)$$

For $j = 2, 3, \dots, y_1 - y_0$, and any $r_1 = W, C, E$, we have:

$$SurvRegM(s, a, y_0, r_0, y_0 + j, r_1) = \sum_{r'=W,C,E} SurvRegM(s, a, y_0, r_0, y_0 + j - 1, r') \exp\{-Z(s, y_0 + j - 1, a + j - 1, r')\} pReg(r', r_1)$$

When $j = y_1 - y_0$ is reached, $SurvRegM(s, a, y_0, r_0, y_1, r_1)$ is obtained.

- $SurvRegII(s, a, y_0, r_0, y_1, r_1)$, defined as the probability that a fish of sex s and age a in year y_0 which is immature in that year and registered at ground r_0 in that year, subsequently survives to year y_1 and remains immature in year y_1 and is registered at ground r_1 in that year.

Because the fish remain registered at their ground of birth before they first mature, it is clear that $SurvRegII(s, a, y_0, r_0, y_1, r_1)$ can only be >0 if $r_1 = r_0$, while it is 0 if $r_1 \neq r_0$.

$SurvRegII(s, a, y_0, r_0, y_1, r_0)$ is calculated as follows:

$$SurvRegII(s, a, y_0, r_0, y_1, r_0) = \exp\left\{-\sum_{i=1}^{y_1-y_0} Z(s, y_0 + i - 1, a + i - 1, r_0)\right\} \frac{1 - mat(s, a + y_1 - y_0)}{1 - mat(s, a)}$$

- $SurvRegIM(s, a, y_0, r_0, y_1, r_1)$, defined as the probability that a fish of sex s and age a in year y_0 which is immature in that year and registered at ground r_0 in that year, subsequently survives to year y_1 and is mature in year y_1 and is registered at ground r_1 in that year.

$SurvRegIM(s, a, y_0, r_0, y_1, r_1)$ can be calculated recursively, going forwards in time year by year, as follows:

For any $r_1 = W, C, E$, we have:

$$SurvRegIM(s, a, y_0, r_0, y_0 + 1, r_1) = \exp\{-Z(s, y_0, a, r_0)\} \frac{mat(s, a + 1) - mat(s, a)}{1 - mat(s, a)} pReg1(r_0, r_1)$$

For $j = 2, 3, \dots, y_1 - y_0$, and any $r_1 = W, C, E$, we have:

$$\begin{aligned} &SurvRegIM(s, a, y_0, r_0, y_0 + j, r_1) = \\ &SurvRegII(s, a, y_0, r_0, y_0 + j - 1, r_0) \exp\{-Z(s, y_0 + j - 1, a + j - 1, r_0)\} \frac{mat(s, a + j) - mat(s, a + j - 1)}{1 - mat(s, a + j - 1)} pReg1(r_0, r_1) \\ &+ \sum_{r'=W, C, E} SurvRegIM(s, a, y_0, r_0, y_0 + j - 1, r') \exp\{-Z(s, y_0 + j - 1, a + j - 1, r')\} pReg(r', r_1) \\ &= \exp\{-\sum_{i=1}^j Z(s, y_0 + i - 1, a + i - 1, r_0)\} \frac{mat(s, a + j) - mat(s, a + j - 1)}{1 - mat(s, a)} pReg1(r_0, r_1) \\ &+ \sum_{r'=W, C, E} SurvRegIM(s, a, y_0, r_0, y_0 + j - 1, r') \exp\{-Z(s, y_0 + j - 1, a + j - 1, r')\} pReg(r', r_1) \end{aligned}$$

When $j = y_1 - y_0$ is reached, $SurvRegIM(s, a, y_0, r_0, y_1, r_1)$ is obtained.

CKMR comparisons

Any CKMR comparison, be it for POP or HSP, involves 2 individuals, which we call I1 and I2.

We will *always condition* on the following covariates of the individuals compared, which we assume known:

- Individual I1: covI1= (y1, a1, s1), i.e. year of sampling, age at sampling, sex.
- Individual I2: covI2= (y2, a2, s2), i.e. year of sampling, age at sampling, sex.

Furthermore, we denote:

- year of birth of I1 (known): $b1 = y1 - a1$
- year of birth of I2 (known): $b2 = y2 - a2$
- ground at which I1 was born (typically unknown, except for larvae samples): $rb1$
- ground at which I2 was born (typically unknown, except for larvae samples): $rb2$

We also condition on the fact that the individuals sampled survived from their birth year to the year in which they were sampled.

The CKMR probabilities are calculated conditional on the population abundances, survival of fish and possible change of ground by the fish, which are part of the PDM description, fecundity of fish and the mixity of fish from different grounds in fisheries.

POP probabilities

In POP comparisons, I1 denotes the potential parent and I2 the potential offspring.

We only consider POP comparisons for pairs where:

- $y1 > b2$, i.e. the potential parent is sampled at least 1 year after the birth year of the potential offspring (since sampling is lethal and to avoid potential problems of time of sampling versus time of spawning within a year)
- The age of the potential parent when the potential offspring was born, $b2 - b1$, is ≥ 3 , as this is the first age of possible maturity.

The following POP probabilities result.

1. If I1 comes from a fishery X1 with “mixture” α_1 , and I2 comes from a larval survey (so rb_2 is known):

The required probability is the product of two factors:

$P(I1 \text{ \& } I2 \text{ are a POP pair} \mid \text{cov}I1, \text{cov}I2, I1 \text{ comes from a fishery X1 with mixture } \alpha_1, rb_2) =$
 $P(I1 \text{ was registered at ground } rb_2 \text{ in year } b_2 \text{ and was mature in year } b_2 \mid \text{cov}I1, I1 \text{ comes from a fishery X1 with}$
 $\text{mixture } \alpha_1) \times P(I1 \text{ is parent of } I2 \mid I1 \text{ was registered at ground } rb_2 \text{ in year } b_2 \text{ and was mature in that year, cov}I1)$

We distinguish two situations regarding the fishery X1 (noting that the difference between the two situations disappears if the age a_1 of I1 when it was sampled corresponds to a fully mature age, i.e. if $mat(s_1, a_1) = 1$):

- If the fishery X1 from which I1 is sampled may catch both mature and immature fish, i.e. an Atlantic fishery, the POP probability becomes:

$$\frac{N_{mat}(s_1, b_2, b_2 - b_1, rb_2) \sum_{r=W,C,E} SurvRegM(s_1, b_2 - b_1, b_2, rb_2, y_1, r) \alpha_1(a_1, r)}{\sum_{r=W,C,E} N(s_1, y_1, a_1, r) \alpha_1(a_1, r)} \frac{Fec(s_1, b_2 - b_1)}{TRO(s_1, b_2, rb_2)}$$

- If the fishery X1 from which I1 is sampled catches only mature fish, i.e. the *Wad* or *Cad* fisheries, then we know that I1 was mature when sampled and the POP probability becomes:

$$\frac{N_{mat}(s_1, b_2, b_2 - b_1, rb_2) \sum_{r=W,C,E} SurvRegM(s_1, b_2 - b_1, b_2, rb_2, y_1, r) \alpha_1(a_1, r)}{\sum_{r=W,C,E} N_{mat}(s_1, y_1, a_1, r) \alpha_1(a_1, r)} \frac{Fec(s_1, b_2 - b_1)}{TRO(s_1, b_2, rb_2)}$$

2. If both I1 and I2 come from fisheries X1 and X2, with mixture α_1 and α_2 , respectively:

Unlike in the previous case, now rb_2 is unknown, and there is one more probability factor to consider:

$P(I2 \text{ was born at ground } rb_2 \mid \text{cov}I2, I2 \text{ from a fishery X2 with mixture } \alpha_2)$

To calculate this probability that I2 was born in rb_2 , we distinguish three situations:

- If the fishery X2 from which I2 is sampled catches only immature fish, i.e. the Croatia juvenile (*CROjuv*) fishery. In this case we know that I2 was immature, and therefore registered at its ground of birth, when it was sampled, obtaining the following formula for the probability that it was born in rb_2 :

$$\frac{N_{imm}(s_2, y_2, a_2, rb_2) \alpha_2(a_2, rb_2)}{\sum_{r=W,C,E} N_{imm}(s_2, y_2, a_2, r) \alpha_2(a_2, r)}$$

- If the fishery X2 from which I2 is sampled catches only mature fish, i.e. the *Wad* or *Cad* fisheries. In this case we know that I2 was mature when it was sampled, and therefore had had the opportunity to change registration ground relative to where it was born, obtaining the following formula for the probability that it was born in rb_2 :

$$\frac{N(s_2, b_2 + 2, 2, rb_2) \sum_{r=W,C,E} SurvRegIM(s_2, 2, b_2 + 2, rb_2, y_2, r) \alpha_2(a_2, r)}{\sum_{r=W,C,E} N_{mat}(s_2, y_2, a_2, r) \alpha_2(a_2, r)}$$

- If the fishery X2 from which I2 is sampled catches both mature and immature fish, i.e. an Atlantic fishery. In this case, the following formula for the probability that it was born in rb_2 is obtained:

$$\frac{N_{imm}(s_2, y_2, a_2, rb_2) \alpha_2(a_2, rb_2) + N(s_2, b_2 + 2, 2, rb_2) \sum_{r=W,C,E} SurvRegIM(s_2, 2, b_2 + 2, rb_2, y_2, r) \alpha_2(a_2, r)}{\sum_{r=W,C,E} N(s_2, y_2, a_2, r) \alpha_2(a_2, r)}$$

It now follows that:

$P(I1 \& I2 \text{ are a POP pair} \mid \text{covI1, covI2, I1 and I2 come from fisheries X1 and X2, with mixity } \alpha1 \text{ and } \alpha2) =$

$$\sum_{rb2=W,C,E} \{ P(I2 \text{ was born at } rb2 \mid \text{covI2, I2 from a fishery X2 with mixity } \alpha2) \times \\ P(I1 \& I2 \text{ are a POP pair} \mid \text{covI1, covI2, I1 from a fishery X1 with mixity } \alpha1, rb2) \}$$

where for the first factor inside the sum (the probability that I2 was born at $rb2$) we need to consider the three situations just described for the fishery X2, and for the second factor inside the sum (the probability that I1 & I2 are a POP pair given that I2 was born at $rb2$) we consider the two situations for I1 described in the previous point. Therefore, six possible situations arise depending on the fisheries X1 and X2 from where I1 and I2 were sampled. Notes on POP probabilities:

- If $\alpha1$ and/or $\alpha2$ correspond to *well-mixed fisheries*, then the $\alpha1$ and/or $\alpha2$ terms disappear from the POP probability formulae
- If $\alpha1$ corresponds to a *pure fishery* on a ground $rf1$, then $\alpha1(a, r) = I[r = rf1]$ and the POP probability formulae simplify accordingly. The same occurs if $\alpha2$ corresponds to a pure fishery on a ground $rf2$.
- The POP probabilities also simplify under heritability and/or faithfulness of the fish to spawning grounds.
- If there was no population structuring in terms of spawning grounds, i.e. if there was just a single ground for the entire population, then the POP probability formulae derived in this document simplify to:
- $\frac{N_{mat}(s1, b2, b2-b1) Surv(s1, b2-b1, b2, y1) Fec(s1, b2-b1)}{N(s1, y1, a1) TRO(s1, b2)}$, if I1 is sampled from a fishery that catches both mature and immature fish.
- $\frac{N_{mat}(s1, b2, b2-b1) Surv(s1, b2-b1, b2, y1) Fec(s1, b2-b1)}{N_{mat}(s1, y1, a1) TRO(s1, b2)}$, if I1 is sampled from a fishery that catches only mature fish.
- where no indices related to ground appear in the equations (as there is a single common ground) and the survival function over multiple year $Surv()$ simplifies accordingly.

HSPs probabilities

We only consider HSP comparisons between individuals I1 and I2 not born in the same year, i.e. $b1 \neq b2$.

There are two possibilities: $b1 < b2$ or $b2 < b1$, so the probability for both cases is presented below.

To avoid double-counting, when the two individuals compared are from the same sampling source (i.e. both are from a larval survey or from a particular fishery), only comparisons where $b1 < b2$ will be made.

It is assumed that it can be distinguished from genetics if two individuals share a mother or if they share a father.

The HSP probabilities derived below are for I1 and I2 sharing a mother. The HSP probabilities for sharing a father are identical, simply replacing “F” by “M” in the formulae below.

1. If both I1 and I2 are from larval surveys (so $rb1$ and $rb2$ are both known):

- $P(I1 \& I2 \text{ have the same mother} \mid \text{covI1, covI2, } rb1, rb2, b1 < b2) =$
Sum over all possible mothers, A, of I1 { $P(A \text{ is the mother of I1} \mid \text{covI1, } rb1) \times P(A \text{ survived to } b2 \text{ and was in } rb2 \text{ at that time}) \times P(A \text{ is the mother of I2} \mid \text{covI2, } rb2, A \text{ was alive and in } rb2 \text{ in year } b2)$ } =
$$\frac{\sum_a N_{mat}(F, b1, a, rb1) Fec(F, a) SurvRegM(F, a, b1, rb1, b2, rb2) Fec(F, a + b2 - b1)}{TRO(F, b1, rb1) TRO(F, b2, rb2)}$$

- P(I1 & 2 have the same mother | covI1, covI2, rb1, rb2, b2 < b1) =

Sum over all possible mothers, A, of I2 { P(A is the mother of I2 | covI2, rb2) x P(A survived to b1 and was in rb1 at that time) x P(A is the mother of I1 | covI1, rb1, A was alive and in rb1 in year b1) } =

$$\frac{\sum_a N_{mat}(F, b2, a, rb2) Fec(F, a) SurvRegM(F, a, b2, rb2, b1, rb1) Fec(F, a + b1 - b2)}{TRO(F, b1, rb1) TRO(F, b2, rb2)}$$

2. If I1 comes from a fishery X1 with mixity α_1 , and I2 is from a larval survey (so rb2 is known):

We will only consider the case where I1 comes from the Croatia juvenile fishery, so that we know I1 was immature and, therefore, was registered at its ground of birth when it was sampled. In this case we have:

- P(I1 & I2 have the same mother | covI1, covI2, I1 from CROjuv fishery, $\alpha_1, rb2, b1 < b2$) =

$$\sum_{rb1} P(I1 \text{ was born in } rb1 | covI1, I1 \text{ comes from CROjuv fishery with mixity } \alpha_1) \\ \times P(I1 \& I2 \text{ have the same mother | covI1, covI2, } rb1, rb2, b1 < b2) = \\ \sum_{rb1, a} \frac{N_{imm}(s1, y1, a1, rb1) \alpha_1(a1, rb1)}{\sum_r N_{imm}(s1, y1, a1, r) \alpha_1(a1, r)} \times \frac{N_{mat}(F, b1, a, rb1) Fec(F, a) SurvRegM(F, a, b1, rb1, b2, rb2) Fec(F, a + b2 - b1)}{TRO(F, b1, rb1) TRO(F, b2, rb2)}$$

- P(I1 & I2 have the same mother | covI1, covI2, I1 from CROjuv fishery, $\alpha_1, rb2, b2 < b1$) =

$$\sum_{rb1} P(I1 \text{ was born in } rb1 | covI1, I1 \text{ comes from CROjuv fishery with mixing } \alpha_1) \\ \times P(I1 \& I2 \text{ have the same mother | covI1, covI2, } rb1, rb2, b2 < b1) = \\ \sum_{rb1, a} \frac{N_{imm}(s1, y1, a1, rb1) \alpha_1(a1, rb1)}{\sum_r N_{imm}(s1, y1, a1, r) \alpha_1(a1, r)} \\ \times \frac{N_{mat}(F, b2, a, rb2) Fec(F, a) SurvRegM(F, a, b2, rb2, b1, rb1) Fec(F, a + b1 - b2)}{TRO(F, b1, rb1) TRO(F, b2, rb2)}$$

3. If both I1 and I2 come from fisheries X1 and X2, with mixity α_1 and α_2 , respectively:

We will only consider the case where I1 and I2 come from the Croatia juvenile fishery, so that we know they were both immature and, therefore, registered at their respective grounds of birth when sampled. In this case we have:

- P(I1 & I2 have the same mother | covI1, covI2, I1 and I2 from CROjuv fishery, $\alpha_1, \alpha_2, b1 < b2$) =

$$\sum_{rb1, rb2} P(I1 \text{ was born in } rb1 | covI1, I1 \text{ comes from the CROjuv fishery with mixity } \alpha_1) \\ \times P(I2 \text{ was born in } rb2 | covI2, I2 \text{ comes from the CROjuv fishery with mixity } \alpha_2) \\ \times P(I1 \& I2 \text{ have the same mother | covI1, covI2, } rb1, rb2, b1 < b2) = \\ \sum_{rb1, rb2} \frac{N_{imm}(s1, y1, a1, rb1) \alpha_1(a1, rb1)}{\sum_r N_{imm}(s1, y1, a1, r) \alpha_1(a1, r)} \times \frac{N_{imm}(s2, y2, a2, rb2) \alpha_2(a1, rb2)}{\sum_r N_{imm}(s2, y2, a2, r) \alpha_2(a2, r)} \\ \times \frac{\sum_a N_{mat}(F, b1, a, rb1) Fec(F, a) SurvRegM(F, a, b1, rb1, b2, rb2) Fec(F, a + b2 - b1)}{TRO(F, b1, rb1) TRO(F, b2, rb2)}$$

- P(I1 & I2 have the same mother | covI1, covI2, I1 and I2 from CROjuv fishery, $\alpha_1, \alpha_2, b2 < b1$) =

$$\sum_{rb1, rb2} P(I1 \text{ was born in } rb1 | covI1, I1 \text{ comes from the CROjuv fishery with mixity } \alpha_1) \\ \times P(I2 \text{ was born in } rb2 | covI2, I2 \text{ comes from the CROjuv fishery with mixity } \alpha_2) \\ \times P(I1 \& I2 \text{ have the same mother | covI1, covI2, } rb1, rb2, b2 < b1) =$$

$$\sum_{rb1,rb2} \frac{N_{imm}(s1,y1,a1,rb1) \alpha1(a1,rb1)}{\sum_r N_{imm}(s1,y1,a1,r) \alpha1(a1,r)} \times \frac{N_{imm}(s2,y2,a2,rb2) \alpha2(a1,rb2)}{\sum_r N_{imm}(s2,y2,a2,r) \alpha2(a2,r)} \\ \times \frac{\sum_a N_{mat}(F,b2,a,rb2) Fec(F,a) SurvRegM(F,a,b2,rb2,b1,rb1) Fec(F,a+b1-b2)}{TRO(F,b1,rb1) TRO(F,b2,rb2)}$$

Notes on HSP probabilities:

- As occurred with POP probabilities, simplifications of the HSP probability formulae occur if $\alpha1$ and/or $\alpha2$ correspond to a *well-mixed fishery*, or to a *pure fishery*.
- The HSP probabilities also simplify under heritability or faithfulness of the fish to spawning grounds.
- If there was no population structuring in terms of spawning grounds, i.e. if there was just a single ground for the entire population, then all the HSP probability formulae derived in this document, for having the same mother, would simplify to:

$$\frac{\sum_a N_{mat}(F,b1,a) Fec(F,a) Surv(F,a,b1,b2) Fec(F,a+b2-b1)}{TRO(F,b1) TRO(F,b2)}$$

where no indices related to ground appear in the equation (as there is a single common ground) and the survival function over multiple year *Surv()* simplifies accordingly.

- Some extra care has to be exercised in the design of HSP comparisons because HSPs look the same genetically as other second-order kin, i.e. GGP (Grandparent-Grandchild) and FTP (Full-Thiatic Pairs, e.g. Aunt-Niece). FTPs can be ignored since they are rare in a random-mating long-lived repeat-breeding species like BFT (for the same reason that Full-Sibs among adults are rare compared to Half-Sibs), but GGPs are common when the animals are born about two generation-lengths apart, becoming less common at shorter birth-gaps. Therefore, it is necessary to select *a priori* the most useful comparisons based on age and sampling-year so as to give low chance of finding GGPs and mistake them for HSPs.
- We will not be able to use all HSPs that are actually present within the comparisons performed. That is because some HSPs (second-order kin) will overlap genetically with⁶ third-order kin (half-aunt-niece, etc.), and the latter need to be excluded to avoid bias. To achieve (almost) total exclusion of unwanted kin, a threshold can be set during kin-finding, with the side-effect that a proportion of true HSPs will be rejected. The false-negative proportion can be estimated outside the CKMR model, based on inspection of the kin-finding results; it cannot be accurately predicted, but in other projects it has typically varied between 10–20%. We allow for false-negatives by working with the probability that a pair will turn out to be a *detected* HSP, i.e. a true HSP whose kinship score also happens to fall above the threshold:

$$P(\text{detected HSP} \mid \text{covariates}) = P(\text{true HSP} \mid \text{covariates}) \times (1 - \text{FalseNegRate})$$

The loss of some true HSPs does not cause bias because it is compensated for (in expectation) by the above equation, but it does reduce the information content of the dataset because there are fewer detected pairs than true pairs. In our calculations and computer code, we have assumed that the false negative rate is 15%.

Design calculations

CKMR design is complicated because of the pairwise aspect; each sample is of literally no value in its own right, and it is only when compared to all other samples that statistical information is obtained. That said, the mathematics of CKMR leads to a powerful shortcut method for predicting CVs, without needing to simulate any datasets or fit any models. There are just two requirements:

- computer code for calculating all the kinship probabilities, conditional on the covariate values that any two samples might have;
- sample size breakdowns.

⁶ Second-order kin pairs are identified based on having a kinship score (a "PLOD", in various other publications) within an expected range. Although true second-order kin-pairs have a distribution of PLODs that is clearly separate from the distributions for first-order kin (e.g. POPs) and for unrelated pairs, there is some overlap with the PLOD distributions of third-order and sometimes of fourth-order kin; there is no reliable way to completely distinguish *all* second-order from third-order kin, although *most* second-order kin are clearly identifiable as such.

Basically, each pairwise comparison between two samples will on average contribute a certain amount to the overall Hessian, from which variances for quantities-of-interest can be calculated by familiar methods. To calculate the individual Hessian contributions, numerical differentiation is used to obtain derivatives of the kinship probabilities, which are then squared. The overall Hessian is then formed by multiplying each Hessian contribution by the number of comparisons that there will be with those particular covariate values (which can be calculated from the sample size breakdowns), and adding it all up. For mathematical details, see Bravington *et al.* (2016b).

4. Performance of multi-year sampling schemes for POPs and HSPs

In this section we address Task 3: “Use the spatial model as an operating model to evaluate the performance of alternative multi-year sampling schemes for POPs and HSPs, suggesting options for the type and number of samples to be collected from different geographic areas/fisheries.”

We have considered a sampling scheme, with samples taken, potentially, from the fisheries shown in **Table 3**. For the fishery samples we assume:

- Proportion by sex: 50% of each sex
- Proportions at age:
 - For the *CROjuv* fishery, we assume the proportion-at-age in the samples is as might be expected in the fishery (approximately 0.67, 0.27, 0.06 for ages 2-4, respectively).
 - For an adult fishery, we assume $(x_{small}, 1 - x_{small})$ for the proportion of samples of ages ≤ 10 and > 10 , respectively, with the proportions-at-age within each of those groups similar to what might be expected from the fishery. To start with, we choose $(x_{small}, 1 - x_{small}) = (0.65, 0.35)$, which is close to what might be expected in the fisheries.
 - Other proportions at age in adult fishery samples could be investigated as part of the design and could vary by fishery.

For the mixing of fish from different grounds in fisheries, we initially assume:

- The samples from *Wlar* are pure from *W* ground
- The samples from the adult fisheries *Wad* and *Cad* are pure from the *W* and *C* grounds, respectively
- The samples from the Atlantic adult fisheries, *ATLad*, are well-mixed
- The samples from the *CROjuv* fishery are not well-mixed (see **Table 1**, where an initial guess for the mixity vector is provided).

POP comparisons for possible inclusion

The following 15 different types of POP comparisons have been programmed in the TMBO code and are available for potential inclusion in the design.

- Each of the adult fisheries (*Wad*, *Cad*, *ATLad*) versus larvae from Balearic survey (*Wlar*)
- Each of the adult fisheries (*Wad*, *Cad*, *ATLad*) versus fish from the Croatia juvenile fishery (*CROjuv*)
- Each of the adult fisheries (*Wad*, *Cad*, *ATLad*) versus fish also from the adult fisheries (the same fishery or a different fishery). In this case, the age range of the fish considered as potential offspring is 3-10.

POP comparisons are only performed for individuals such that the potential parent is sampled at least one year after the birth year of the potential offspring, and the age of the potential parent in the birth year of the potential offspring is at least 3.

HSP comparisons for possible inclusion

The following comparisons have been programmed in the TMBO code and are available for potential inclusion in the design. These are 3 types of comparisons for MHSP (sharing a mother) and 3 types of comparisons for FHSP (sharing a father), i.e. 6 types of comparisons in all.

- *Wlar* versus *Wlar*
- *CROjuv* versus *Wlar*
- *CROjuv* versus *CROjuv*

HSP comparisons are only performed between individuals born in different years, i.e. $b_1 \neq b_2$. In the case of *Wlar* versus *Wlar* comparisons or *CROjuv* versus *CROjuv* comparisons, only comparisons where $b_1 < b_2$ are considered, to avoid double counting. In the case of *CROjuv* versus *Wlar* comparisons, both $b_1 < b_2$ and $b_1 > b_2$ are considered, where b_1 denotes the birth year of the fish taken from the *CROjuv* fishery and b_2 that of the larva.

Number of samples per year and expected number of kin pairs

We initially consider a sampling scheme with the number of samples per year as shown in **Table 4**. This sampling scheme results in 111000 samples in all (63000 from the *Wlar* survey and 12000 from each fishery).

For the CKMR statistical analysis below (expected number of “meaningful” kin pairs, and calculation of precision of estimates), the number of samples from the larval survey have been multiplied by an arbitrary 0.5 factor, to account for intra-cohort sibship discussed near the start of this report. However, **Table 4** shows the number of samples that would be collected and genotyped, as this is what will affect logistics and costs.

Assuming that the 15 types of POP comparisons and 6 types for HSPs comparisons described above are performed, this design results in 2,802,403,050 meaningful comparisons and 1654 expected meaningful kin pairs (473 POPs and 1181 HSPs, rounding to nearest integer). The breakdown of expected kin-pairs is shown in **Table 5**.

The expected number of meaningful POP pairs can alternatively be presented in a plot versus the age of the parent in the year of birth of the potential offspring, as seen in **Figure 4**. It suggests that a reasonable choice of units for expressing TRO, might be as “equivalent number of 10-year-old fish”.

Precision of estimates from CKMR analysis

The statistical model to conduct the estimations of quantities of interest would be based on the PDM described in Section 2 and Poisson likelihoods for the observed numbers of close-kin pairs using the CKMR probabilities derived in Section 3.

As already noted at the end of Section 3, calculating the precision of the resulting estimates does not require simulation of potential CKMR datasets, because the Poisson likelihood allows for the calculation of the Hessian numerically. Hence, the precision of the estimates of various quantities of interest can be calculated from the numerically derived Hessian and the delta method for transformations of parameters.

One main focus of the CKMR analysis for BFT-E is to estimate population abundance in absolute terms. CKMR only gives direct information on adult abundance, which may be expressed in several alternative ways, as shown in **Table 6**. The table indicates low CVs for the estimates of adult population biomass, whether expressed as Biomass(5+) or SSB or TRO equivalent number of 10 year-old fish. It is, however, important to realize that estimates from different years are quite correlated here; an “average” CV of 15% from CKMR is very good, but it is nothing like having independent annual estimates of absolute abundance with 15% CVs (There is of course no method on the planet that could accomplish the latter.)

CKMR data also permit the estimation of other population quantities of interest, such as relative fecundity at age and total mortality Z . As an illustration, the ratio of fecundity at age 15 versus the fecundity at age 5 would be estimated with a CV of 0.14, whereas the standard deviation of average Z (ages 5-20) is presented in **Table 7**.

Precision of estimates from CKMR analysis, using only data until 2026

The purpose of this exploration is to gain understanding of what might be achievable by 2027, i.e. using only samples going to 2026.

In this case, the number of meaningful comparisons is 495,562,054, from which 323 meaningful kin pairs (80 POPs and 243 HSPs, rounding to nearest integer) are expected. The breakdown of expected kin pairs is in **Table 8**.

The results in **Table 9** indicate considerably higher CVs for the estimates of Biomass(5+) compared with the case when data until 2030 are used (**Table 6**). Comparing **Table 9** and **Table 6** we can see that extending the sampling scheme to 2030 reduces considerably the CVs of the Biomass(5+) estimates for the entire time period (i.e. for all years since 2014).

Precision of estimates from CKMR analysis, using only data until 2026, shifting the sampling intensity towards larger fish in the fisheries

Here we continue considering only CKMR data until 2026, to gain an understanding of what may be achievable by 2027.

As indicated at the beginning of this section, for an adult fishery, we assume $(x_{small}, 1 - x_{small})$ for the proportion of samples of ages ≤ 10 and > 10 . We now choose $(x_{small}, 1 - x_{small}) = (0.35, 0.65)$, to investigate the effect of shifting the sampling effort in fisheries towards larger fish (as larger fish are more fecund and, therefore, more likely to be parents and provide POP matches).

In this case, the number of meaningful comparisons is 499,063,429, from which 352 meaningful kin pairs are expected, somewhat more than the 323 expected in the previous case. Comparing **Table 10** and **Table 8**, we can see that the increase in the number of expected kin pairs is in the POPs, whereas the expected number of HSPs remains unchanged. The CVs of the Biomass(5+) estimates (**Table 11**) are slightly lower than those in the previous case (**Table 9**).

Precision of estimates from CKMR analysis, with data until 2030, halving the sample sizes

Here we go back to the situation described at the beginning of this section (**Table 3**), but dividing all sample sizes (past and future) in **Table 4** by 2.

In this case, the number of meaningful comparisons is 700,600,763, from which 414 meaningful kin pairs are expected. This is 1/4 of the previous number, which we would expect from basic properties of CKMR: all else being equal, the number of kin-pairs increases with the square of the sample size, and the CV decreases with the reciprocal of the sample size (in contrast to most statistical settings, where it is the reciprocal square root that affects CV).

Tables 12 and **13** present the results, indicating CVs for the estimates of Biomass(5+) which are indeed twice as large as those shown in **Table 6**.

5. Detecting departures from baseline hypotheses about population structure

In this section we address Task 4: “Use the spatial model to explore how the data might reveal departures from “baseline” hypotheses made for item 3; for example, that two or three of the subpopulations are fully mixed in the Atlantic and that there is spawning site fidelity.”

As requested in the terms of reference, here we use the model developed in the previous sections to investigate how the observed kin pairs can provide information about population structure and spawning site fidelity.

We consider the same sampling settings as at the beginning of Section 4, which are described in **Tables 3** and **4**. The sampling scheme results in the expected kin pairs shown in **Table 5**, which we repeat in the top lines of **Table 14** (i.e. $pf = 0.9$, $pf1 = 0.9$).

The rest of the lines in **Table 14** show the expected numbers of kin pairs under other possibilities about population structure, based on alternative values of the parameters pf and $pf1$, which were introduced in Section 2. As noted in Section 2, $pf \approx 1$ corresponds to faithfulness (the fish would always spawn in the same ground, although it is not necessarily their ground of birth) and $pf1 = 1$ corresponds to heritability (i.e. the first time the fish choose a ground, when they first mature, they choose their ground of birth). The more relevant values informing about population structure are highlighted with bold values in the table. Discussion of the results follows next.

If $pf \approx 1$ and $pf1 \approx 1$ (faithfulness and heritability), the fish always spawn in their ground of birth, resulting in 3 separate biological populations. In this case, no POP or HSP matches occur between individuals from different grounds. Therefore, no POP or HSP matches can occur from two individuals obtained from two different sampling sources which are both “pure” from a single ground, as is the case for the *Wlar* survey (purely *W* ground), and is also assumed to be the case for the *Wad* and *Cad* fisheries (pure *W* and *C* grounds, respectively). This explains the 0 POP values in **Table 14** for this case.

We recall that *CROjuv* and *ATLad* fisheries are assumed to be not pure from a single ground, so the argument above does not apply to fish sampled from those sources. If *CROjuv* was a “pure” fishery from the *C* ground, then, under faithfulness and heritability, we would find no POPs either between fish from *CROjuv* and the *Wad* fishery and no HSPs between *CROjuv* and *Wlar*. **Table 14** indeed shows 0 values in the corresponding cells.

Under faithfulness ($pf \approx 1$) without heritability ($pf1 < 1$), no POP matches occur between *Cad* fish and *Wlar*, as the *Cad* fish must always have spawned in the *C* ground. However, the lack of heritability makes it possible to have POP matches between *Wad* and *Cad* fish, as the fish may have been born at a ground different from the one they use as spawners. In line with this, **Table 14** shows in the lines corresponding to $pf \approx 1$ and $pf1 \approx 0$, a 0 for the probability of a POP between *Cad* and *Wlar*, but values >0 for the probabilities of POP between *Cad* and *Wad*. The table also shows a strongly reduced number of *Wad* – *Wad* and *Cad* – *Cad* POPs, when compared to the faithfulness with heritability case.

As before, since *CROjuv* and *ATLad* fisheries are assumed to be not pure from a single ground, the argument above does not apply to fish sampled from those sources. However, if *CROjuv* was a pure fishery from the *C* ground (and bearing in mind that the fish taken in the *CROjuv* fishery are assumed to be juveniles and, hence, still registered at their ground of birth when they are sampled), the number of POP matches between *Wad* and *CROjuv* fish would be expected to be 0, and the number of HSP matches between *Wlar* and *CROjuv* would also be expected to be 0, as can indeed be observed in **Table 14**.

Cases with lower values of pf result in a fairly mixed population, with patterns of expected kin pairs that do not differ very strongly between samples taken from different sources. This can be seen in the last 2 cases shown in **Table 14** (corresponding to $pf = 0.5$ and $pf \approx 0$, respectively).

It is worth noting that the Atlantic fisheries contribute no information on faithfulness and heritability. It is precisely because they are likely to be well-mixed (at the minimum, this should be the case for the Portuguese traps) and, thus, ideal for estimating overall abundance, that they are not informative for within-Med spatial structure (though they do have a role in checking other assumptions; see Discussion section). The information in **Table 14** comes from comparisons between the two adult fisheries within the Med and the two different juvenile fisheries.

The size of the numbers in **Table 14** is also important, not just whether we expect zero or something positive. The actual number of kin-pairs in each category (i.e. cell of the table) should be Poisson-distributed about those expected values. Hence, if one of the expected values was, say, 2 for the case $pf \approx 1$ and 0 for $pf \approx 0$, then seeing a 0 in that category would only be very weak evidence against faithfulness (p -value about 13%). But the values in the table are actually quite large; if the expected value is 10 then there is no way that a 0 could happen just by chance. Thus, even if the sampling setup has enough power qualitatively to reveal effects – which it does here – it is still necessary to have large enough sample sizes to those make effects realistically detectable.

6. Discussion

Model caveats and future development

As noted in the Introduction, we have made some substantial simplifications for the sake of having a tractable Design task.

1. The model is completely age-based, i.e. we have coded the population-dynamics, CKMR probabilities and sampling scheme as if all phenomena were age-based. In reality, though, most biological and fishing processes are determined more by length than by age per se. A full CKMR analysis of real data (as with SBT) should use both length and age, and would probably need to fit a growth curve internally. However, such a model becomes quite complicated. It is not obvious whether an age-driven approximation will over- or under-predict CVs compared to a full model – and in part, it will depend on what proportion of BFT-E samples are aged, presumably by epigenetic methods – but we expect that the effect is not massive; even an age-only model is enough to capture the most important aspects of fish biology here, which is that they grow through adulthood, become more fecund as they do so, and may also change their catchability as they do so.
2. A full CKMR analysis should use catch data (disaggregated by length), and should not need to assume anything about selectivity, which does not appear in the kinship probability equations that underpin CKMR. Once catches are included, it becomes possible to estimate adult natural mortality (M), or at least its average level (see previous documents). We expect that a full BFT-E model will ultimately deal with catch-at-size in that way, but that would be completely impractical at this point in a Design study. Aside from the sheer number of BFT-E fisheries, there is the additional complication of not knowing how the catch in most of them might be split amongst the subpopulations. Instead, we have chosen to work just with Z , assuming a known selectivity-at-age pattern for the fisheries and known M , but estimating the overall level of fishing mortality (F). We think this should give *roughly* the same amount of estimation freedom as a fully catch-based model would have, but it is not possible to be completely sure.

3. We have not included any composition data (neither age-at-length, which should be robust to selectivity, nor length itself, which is not). In practice, we would expect to use at least the first of these in a CKMR model (for estimating recent recruitment), so we have deprived the model of some useful data. On the other hand, we have treated selectivity as known, whereas in practice it would have to be estimated – which is where length composition data would be required. Since composition data does not provide any direct information on absolute abundance, the effect of this approximation on the CV of abundance is probably not enormous, although the effect on other parameters such as Z or M is harder to predict.
4. We have made a simple *ad hoc* adjustment to effective sample size to the Balearic larval samples, in order to account for intra-cohort sibship. Dealing with this properly will require significant adjustment to the underlying CKMR machinery, using techniques developed for BFT-W. The actual impact on variance remains unknown until one or two full years of Balearic samples have been genotyped.

Effect of different spatial-structure assumptions on precision

For Task 3 (Section 4), we have only considered one scenario for the combination of faithfulness, heritability, mixity of *CROjuv* samples and subpopulation abundances. How much are the CVs likely to differ if the scenario details differ from reality? There are two main aspects to consider: first overall abundance, and second everything else (spatial structure, subpopulation abundances).

All else being equal, it is a general property of CKMR that CVs will scale with the reciprocal-square-root of abundance, and with the reciprocal of sample size. In other words, if the true abundance is 4 times higher than we have assumed, the CVs will be 2 times higher for the same sample size; i.e. to keep the same precision reported in the tables, sample sizes would need to double. This is a very important and unavoidable source of uncertainty in CKMR design; to do an ideal design, we would need a fairly precise abundance estimate beforehand, in which case there might not be an interest to conduct a CKMR analysis. Therefore it is crucial to plan for flexibility in sampling over time, as noted later on.

However, if the spatial structure and/or subpopulation abundances are not as assumed in Task 3, then not all else is equal and some CVs will change. Nevertheless, the precision of the aggregate abundance estimate, which for BFT-E is the quantity of most interest, is primarily determined by the number of POPs found between the Atlantic fisheries and the *Wlar* and *CROjuv* fisheries. That comparison is unaffected by spatial structure within the Med spawning grounds, so we expect the CV of the overall abundance estimate to be fairly stable. While it is true that the precision of the estimates of parameters that describe faithfulness and heritability will depend on their true values, as well as on the split between subpopulation sizes, those parameters are not the main focus of design.

Bias

This document deals extensively with the precision that might be expected for the estimates of various quantities, but makes no quantitative mention of bias, despite spatial structure being a fairly obvious potential source of bias in CKMR for a species like BFT-E. The reason is that we have tried to build a CKMR model that is flexible enough to estimate the parameters of a spatially-structured model. The basic properties of maximum-likelihood estimation then imply that the results will be approximately unbiased, as long as there are enough data to estimate all parameters with reasonable precision (which it turns out there are, at least with the sampling scheme shown in Section 4).

However, bias would result if we were to fit a simpler model, e.g. a non-spatial CKMR model, to a situation that violated its assumptions. One obvious example would be if there was persistent spatial structure but we aggregated all adult samples regardless of which fishery they came from, and likewise for all juvenile samples, and then simply applied a non-spatial CKMR model. Because the aggregate adult samples would overweight some subpopulations, and the same would occur with the juvenile samples, the spatially-naïve kinship probabilities for the aggregate samples would not correctly represent the true kinship probabilities (which must, if there is persistent spatial structure, involve the probability that the two individuals being compared come from the same subpopulation, since otherwise they cannot be a POP). Applying a spatially-naïve model would certainly lead to bias in that case, and that is why we are not aggregating samples or using a simple model.

One area where we have not tried to build a spatially-explicit model, but instead have opted to make a working assumption, concerns how well-mixed the Atlantic fisheries are. In this respect our model could theoretically have some bias, but as the next subsection explains, we would not expect serious problems.

Checking for good mixing in the Atlantic fisheries

Our model has specific parameters that describe the extent of faithfulness and heritability, and we have shown that these can be estimated quantitatively – which tests the assumptions automatically. There is really no convincing data that would justify a strong prior belief in any particular values of faithfulness and heritability, so it seems sensible to estimate these parameters, which is why we have a model with explicit spatial structure.

Our results do not consider poorly-mixed Atlantic samples (e.g. if 99% of *W* adults migrated to the Atlantic annually, but only 70% of *C* adults and 30% of *E* adults did so). Satellite-tag data suggest that such behaviour is unlikely for *W* and *C* adults (and at least some older *E* adults have also been seen migrating, though sample sizes are very limited). It seems reasonable to *start* with a working assumption that the Atlantic fisheries are well-mixed, and try to check at a later stage whether this is a justifiable approximation; only if there is good evidence against it, would it be worth developing a more complex model (and by then there might also be more satellite-tag data). So the question is whether there will be enough POPs to check the assumption, with **Table 5** providing the key reference here.

A first way to check the good mixing in the Atlantic fisheries is to see whether the various Atlantic fisheries (Portuguese traps, Canada, Norway...) have similar rates of POPs when each of those Atlantic fisheries is compared to one particular juvenile fishery, e.g. *Wlar* (after allowing for different age compositions in the Atlantic adult samples and after removing BFT-W fish). Differences in the rates of POPs could indicate, for example, that *W* juveniles tend to prefer Canada whereas *C* juveniles prefer Norway, in which case the Canada and Norway fisheries would not be well-mixed. According to **Table 5**, by 2030 we might expect about 60 POPs in total between the three *ATLad* fisheries and *Wlar*: so about 20 per Atlantic fishery, if Atlantic samples were split evenly between the 3 Atlantic fisheries (which they may well not be). With an expected value of 20 POPs, observed values below about 13 or above about 35 are strongly significant; thus, true differences would need to be of the order of $\pm 40\%$ to have a good chance of statistically-significant detection. Even if a strong difference appeared between, say Canada and Norway rates of *Wlar* POPs, it is hard to imagine that *W* & *C* would *not* be well-mixed in the Portuguese trap fishery, because that is the only way out of the Mediterranean. It would be possible to expand the CKMR model to allow different feeding preferences within the Atlantic depending on subpopulation, at least as long as there are *some* well-mixed samples to keep everything anchored (e.g. from Portuguese traps). Note that the *CROjuv* samples may be less informative about Atlantic feeding preferences, because they may comprise a mix of *W*, *C*, and *E* juveniles.

A second way to check whether the Atlantic fisheries are well-mixed, is to examine whether the two juvenile fisheries (*Wlar* and *CROjuv*) have similar rate of POPs, when compared against the combined *ATLad* samples (after adjusting for differences in juvenile birth year). The question of interest here is whether *E* adults are migrating into the Atlantic at the same rate as *W* and *C* adults. If that is true, and if also *E*-born juveniles make up a substantial proportion of the *CROjuv* samples, then we would expect to see fewer *ATLad* – *CROjuv* POPs than under the working assumption of full Atlantic mixing. **Table 5** shows about 60 and 33 *ATLad* POPs expected from *Wlar* and *CROjuv*, respectively (more from *Wlar* because sample sizes there are much higher). A number for *ATLad* – *CROjuv* much lower than 33 (say, 23 or less) would be strongly significant evidence against good-mixing. Of course, those two numbers will change substantially once a CKMR model has been fitted, but the rough magnitudes are the important thing at this point. An expected value as high as 33 is quite reasonable for detecting failures (something that would not be possible with an expected value of 3.3, for example), but in the specific context of BFT-E, the "effect size" between a significant result at 23 and no effect at 33 is about 30%, which would correspond to a huge difference in behaviour between *E* adults and *W* + *C* adults (as well as a high number of *E* adults overall, and a high proportion of *E* juveniles in Croatia). If the data was subsetted even more finely, for example to check whether POP rates at age are similar between *Wlar* and *CROjuv* (the alternative hypothesis now being that young *E* adults, but not old ones, are less likely to leave the Med), expected values would be substantially reduced, and it would require a fairly drastic failure of the null hypothesis to get a significant result. However, the qualitative point remains that (if the *CROjuv* samples contain *W*, *C*, and *E*-born animals) there will eventually be enough data to resolve such questions if a CKMR study goes on long enough.

Diagnosing spatial structure requires substantial sample sizes, and thus may take some time. By 2027, only 12 *ATLad* – *Wlar* and 6 *ATLad* – *CROjuv* POPs might be expected (**Table 8**) so, unless sampling levels are much higher than in Section 4, and/or total abundance is much lower than assumed, there is no chance of detecting even fairly strong departures from Atlantic good-mixity.

This discussion is fairly complicated and highly conditional; basically, it all depends what it is found when the CKMR are obtained and analysed. The checks could be broken up in ways different to those described (e.g. potentially looking at age-breakdowns of POPs) but the more fine-grained the investigation is, the fewer POPs

there will be to check it on, and only really strong effects could be reliably detected. The basic message here is that strong departures from Atlantic good-mixing might be detectable by, say, 2030 under the sampling scheme in Section 4, but there is no chance of detecting them by 2027. Fortunately, *weak* departures from good-mixity are unlikely to trouble the aggregate estimates much anyway; and there is a reasonable *a priori* basis for not expecting major departures from well-mixing in the Atlantic, at least between the *W* and *C* subpopulations.

Age data

Some idea about sample age is always vital in CKMR. Depending on the biology and the particular sample, it might be enough to identify the life-stage, or it might be enough to have indirect information (e.g. via length), or it might be important to have a direct estimate nowadays from epigenetics ("DNAge"; see recent report to ICCAT on this topic – reference?), with or without appreciable measurement noise (otoliths are not an attractive proposition for BFT-E). Our model assumes all ages are known exactly, and all phenomena (fecundity etc) are linked purely to age. Reality, and the model that we expect will ultimately be developed for application to real BFT-E data, does not work quite like that. Accurate age estimates are most important for younger fish that are to be used as potential-offspring in POP comparisons, and/or as potential HSPs, because all the probabilities are conditional on the birth-year of the samples; uncertainty about birth year substantially diminishes the information content.

For adults (potential parents), age is still important but less critical. In particular, fecundity is driven by length rather than age, and accurate length measurements *may* be easy to obtain for the fisheries discussed here. The relevant driver is not the length of an adult sample when that fish is killed, but rather the length it would have had at the birth of the potential offspring to which it is being compared. For that, it helps also to know the adult's age at sampling, because then its past lengths can be back-projected based on individual growth curves. However, if back-projection only covers a few years, then length alone at sampling may give a usefully precise back-projection.

A further consideration is that it will likely be desirable to incorporate growth-curve estimation (and variance of length at age, which is important in CKMR) into the overall model, and for that a reasonable number of adults should be aged as part of ongoing sampling.

For SBT (where otoliths rather than DNAge are used, at least for now), a reasonable approach has been to age a subset of adult samples annually regardless of whether they are parents or not, and also to age every adult that is found to be a parent. For juvenile samples, SBT is fortunate in that almost all are known to be age-3 (based on vertebral slicing of a subset).

It remains to be seen what the best option may be for BFT-E. It may not be necessary to DNAge *every* adult sample, but it is probably a very good idea to DNAge at least all *CROjuv* samples, since several ages are caught together and length is not a *reliable* predictor of age even in the range 2–4. The amount that should be done will depend on the unit cost of the procedure (noting that extracted DNA is available for free, as part of CKMR genotyping). This might form the subject of further design work in future, although a full length-and-age model would be needed.

General notes on sampling strategy

- It is possible to estimate BFT-E abundance by heavily sampling just two fisheries: Portuguese traps and Balearic larvae being one way to do it. Nevertheless, it seems preferable to spread the sampling across *a few more* selected ones (but not too many) because:
 - that is the only way to determine basic spatial structure, i.e. the extent of faithfulness and heritability, and the abundance split between the subpopulations. This basic biological information is of at least qualitative importance for management;
 - spreading the sampling reduces the burden on individual fisheries (although that may not be limiting) and reduces the risk if one sampling source ceases to be available;
 - Balearic larvae will be subject to some unknown efficiency loss because of intra-cohort sibship, so it would be safer not to put all juvenile sampling effort exclusively there.
 - As noted in previous reports, it is equally undesirable to have small sample sizes from *too many* partly-mixed fisheries, because each one brings its own set of parameters to estimate (based on few kin-pairs), modelling is rendered very complicated, and there is less opportunity to check assumptions because kin-pairs are too disaggregated.
- In the future, once the spatial structure, etc. has been worked out, it might be possible to streamline sampling onto fewer fisheries. But unless there is a slightly wider spread at the start, as we have proposed, it will not be possible to check assumptions.

- It is worth trying to sample intensively at the start (but only once the physical logistics have been smoothed out). If the initial round of genotyping yields enough kin-pairs (i.e. if the population is smaller than assumed) then it may not be necessary to genotype all the samples that have been collected. But if the abundance turns out to be higher, and if the extra samples were not collected in the first place, there is no way to go back in time to collect them later.
- It is crucial to realize that sampling levels might need to be adjusted as a CKMR project goes on; precision depends on how many kin-pairs are found, and that will depend on true abundance as well as sample size. Although it is possible to suggest guidelines based on *assumptions* about abundance, etc., as we have done here, we cannot *know* what the true abundance is beforehand — otherwise we would perhaps not be conducting a CKMR analysis at all⁷.

7. Conclusions

- Given sampling levels that seem quite feasible logistically, from a small number of selected fisheries (and a larval survey), then by 2030 we might expect very good precision on adult abundance (~10% CVs) and on Z (in effect on M) – under reasonable working assumptions about spatial structure and current abundance.
 - There should also be enough kin-pairs of particular types to check assumptions about spatial structure, e.g. extent of spawning site fidelity.
- Useful CVs on aggregate abundance might even be achieved in time for SCRS 2027, but there will not be not enough kin-pairs to check most spatial structure assumptions.
- The next steps would be to refine the design (i.e. consider alternative sampling schemes), based on discussions of:
 - desirable CVs and timeframes;
 - sampling logistics.
- This additional work could be completed by the end July. It would be a necessary part of a complete, coherent proposal for an BFT-E CKMR study (or at least the first couple of years, since revisions might become necessary as information accrues), alongside finalized, costed, proposals for genotyping (nuclear, mitochondrial, other e.g. BFT-W/EABFT assignment) and DNAgeing.

8. Acknowledgments

The authors are grateful to Ana Parma for very helpful insights during the development of this work and the write-up of this report.

This work was carried out under the provision of the ICCAT. The contents of this document do not necessarily reflect the point of view of ICCAT, which has no responsibility over them, and in no ways anticipate the Commission’s future policy in this area.

This work was conducted within the ICCAT GBYP Phase 13 and partially funded by the European Union through the EU Grant Agreement No. 101133291.

⁷ This is exactly what happened with SBTuna; the initial sampling design (based on the assumed assessment at the time) turned out after a couple of years to be generating far too few POPs, so it was clear that abundance was higher than assumed. The sample size was increased, by extending the project for a few years, and really good precision was obtained in the end. It is by no means inevitable that sample sizes will have to increase, though; if the SBT results had yielded more kin-pairs than expected, then the initial study could have stopped earlier, although the value of CKMR for ongoing monitoring would likely have seen a continuation.

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Table 1. Parameters treated as unknown (i.e. estimated) and fixed (not estimated) in the CKMR analysis.

<i>Parameters estimated in the CKMR analysis</i>	<i>Initial guess</i>
$Rmed(r)$ for the 3 grounds ($r = W, C, E$)	400,000, for each ground
log-normal recruitment deviations for each year and ground: $\log(Rdev(y, r)) \sim N(0, \sigma_R = 0.6)$, resulting in 51 parameters	For years 2014-2021: values similar to the SS3 2022 BFT-E assessment estimates. After 2021: 0.
Slope for $\log(\text{population abundance at age})$ in initial year $y = Yinit$	-0.265
log-normal deviations for the abundance-at-age (ages 3-30+) in the initial year: $\log(N_Yinit_dev(a)) \sim N(0, \sigma = 0.6)$, resulting in 28 parameters	0, for all ages
pf , probability of staying in same ground as in previous year	0.9
Probability $g(r)$ of the 3 grounds ($r = W, C, E$) (2 independent parameters, as the sum over the 3 grounds = 1)	(0.30, 0.40, 0.30)
$\gamma(s)$, the exponent of the fecundity transformation, assuming the same value for both sexes	1
$F(r)$ for the 3 grounds ($r = W, C, E$)	1, for each ground
Mixity vector of fish in the Croatia juvenile fishery for the 3 grounds ($r = W, C, E$) (2 independent parameters, summing to 1 over the 3 grounds)	(0.167, 0.667, 0.167)
<i>Fixed parameters (not estimated):</i>	
$pf1$, probability of staying in the same ground as in previous year, the first year in which a fish matures	0.9
$M(a)$, natural mortality*	0.266 at age 2 and decreasing progressively to 0.099 for ages 22 and older (Table 11 of Anon. 2022)
$mat(s, a)$, maturity*	0, 0.25, 0.5 and 1 for ages 2, 3, 4 and 5+ (Table 10 of Anon. 2022)
$weight(s, a)$, weight*	See Table 11 of Anon. 2022
$F(s)$	1, for both sexes
$Sel(a, r)$, selectivity-at-age for each of the 3 grounds	As in Figure 3
$F(y)$	Described in text above
Mixity vector of fisheries different from the Croatia juvenile one	Described in text above

*From 2022 SS3 BFT-E assessment

Table 2. SSB values corresponding to the initial guesses for parameters and variables in the CKMR design work.

	2014	2015	2016	2017	2018	2019	2020	2021	2022
SSB (thousand t)	287	316	347	382	418	452	485	519	538
	2023	2024	2025	2026	2027	2028	2029	2030	
SSB (thousand t)	557	557	551	541	529	515	502	490	

Table 3. Sampling sources, with year and age ranges, considered in potential sampling schemes for CKMR.

	<i>Larval survey</i>	<i>Juvenile fishery</i>	<i>Adult fisheries</i>		
	Balearics: <i>Wlar</i>	Croatia: <i>CROjuv</i>	West Med: <i>Wad</i>	Central Med: <i>Cad</i>	Atlantic: <i>ATLad</i>
Years	2019-2030 (exc. 2021)	2025-2030	2025-2030	2025-2030	2025-2030
Age at sampling		2-4	3-28	3-28	3-28

Table 4. Number of samples per year in initial sampling scheme for CKMR.

<i>Number of samples per year</i>					
	<i>Larval survey</i>	<i>Juvenile fishery</i>	<i>Adult fisheries</i>		
	Balearics: <i>Wlar</i>	Croatia: <i>CROjuv</i>	West Med: <i>Wad</i>	Central Med: <i>Cad</i>	Atlantic: <i>ATLad</i>
2019-2024	3000 (excluding 2021)	0	0	0	0
2025-2030	8000	2000	2000	2000	2000

Table 5. Expected number of meaningful kin pairs: (a) POPs, (b) HSPs, obtained with initial sampling scheme for CKMR.

<i>POPs</i>		<i>Potential Offspring</i>					<i>HSPs</i>			
		<i>Wlar</i>	<i>CROjuv</i>	<i>Wad</i>	<i>Cad</i>	<i>ATLad</i>		<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>
Potential Parent	<i>Wad</i>	164	21	25	7	14		<i>Wlar</i>	<i>Wlar</i>	<i>CROjuv</i>
	<i>Cad</i>	15	53	7	21	13	MHSP	467	89	34
	<i>ATLad</i>	61	33	13	13	13	FHSP	467	89	34

Table 6. Coefficient of Variation (CV) of estimates of BFT-E adult population abundance (measured in alternative ways), obtained with initial sampling scheme for CKMR.

<i>CV of estimates by year:</i>										
	2014	2015	2016	2017	2018	2019	2020	2021	2022	
Biomass (5+)	0.37	0.32	0.27	0.22	0.18	0.16	0.14	0.12	0.12	
SSB	0.35	0.30	0.25	0.21	0.18	0.15	0.13	0.12	0.12	
TRO (Equivalent no. of 10-year-old fish)	0.36	0.31	0.26	0.22	0.18	0.16	0.14	0.13	0.12	
	2023	2024	2025	2026	2027	2028	2029	2030		
Biomass (5+)	0.12	0.12	0.12	0.12	0.13	0.13	0.14	0.14		
SSB	0.11	0.11	0.12	0.12	0.12	0.13	0.13	0.14		
TRO (Equivalent no. of 10-year-old fish)	0.12	0.12	0.12	0.12	0.12	0.13	0.13	0.14		

Table 7. Standard deviation of estimates of total mortality (Z), obtained with initial sampling scheme for CKMR.

<i>Standard deviation of estimates of average Z (ages 5-20) by year:</i>									
2014	2015	2016	2017	2018	2019	2020	2021	2022	
0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	
2023	2024	2025	2026	2027	2028	2029	2030		
0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03		

Table 8. Expected number of meaningful kin pairs: (a) POPs, (b) HSPs, obtained with initial sampling scheme for CKMR but using data only until 2026.

<i>POPs</i>		<i>Potential Offspring</i>					<i>HSPs</i>			
		<i>Wlar</i>	<i>CROjuv</i>	<i>Wad</i>	<i>Cad</i>	<i>ATLad</i>		<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>
Potential Parent	<i>Wad</i>	32	4	3	1	2		<i>Wlar</i>	<i>Wlar</i>	<i>CROjuv</i>
	<i>Cad</i>	3	9	1	2	1	MHSP	104	15	3
	<i>ATLad</i>	12	6	1	1	2	FHSP	104	15	3

Table 9. Coefficient of Variation (CV) of estimates of BFT-E adult population abundance (measured as biomass of ages 5 and older), obtained with initial sampling scheme for CKMR but using data only until 2026.

<i>CV of Biomass(5+) estimates by year:</i>													
2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	2025	2026	2027
0.69	0.60	0.52	0.44	0.37	0.33	0.30	0.29	0.29	0.29	0.30	0.32	0.34	0.37

Table 10. Expected number of meaningful kin pairs: (a) POPs, (b) HSPs, obtained with initial sampling scheme for CKMR but using data only until 2026 and $x_{small} = 0.35$.

<i>POPs</i>		<i>Potential Offspring</i>					<i>HSPs</i>				
		<i>Wlar</i>	<i>CROjuv</i>	<i>Wad</i>	<i>Cad</i>	<i>ATLad</i>		<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>	
Potential Parent	<i>Wad</i>	47	5	3	1	1		<i>Wlar</i>	<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>
	<i>Cad</i>	4	13	1	2	1	MHSP	104	15	3	
	<i>ATLad</i>	18	8	1	1	1	FHSP	104	15	3	

Table 11. Coefficient of Variation (CV) of estimates of BFT-E adult population abundance (biomass of fish of ages 5 and older), obtained with initial sampling scheme for CKMR but using data only until 2026 and $x_{small} = 0.35$.

<i>CV of Biomass(5+) estimates by year:</i>													
2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	2025	2026	2027
0.66	0.58	0.50	0.42	0.36	0.32	0.29	0.28	0.28	0.28	0.29	0.30	0.32	0.33

Table 12. Expected number of meaningful kin pairs: (a) POPs, (b) HSPs, obtained with initial sampling scheme for CKMR but halving the sample sizes in Table 4.

<i>POPs</i>		<i>Potential Offspring</i>					<i>HSPs</i>				
		<i>Wlar</i>	<i>CROjuv</i>	<i>Wad</i>	<i>Cad</i>	<i>ATLad</i>		<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>	
Potential Parent	<i>Wad</i>	41	5	6	2	3		<i>Wlar</i>	<i>Wlar</i>	<i>CROjuv</i>	<i>CROjuv</i>
	<i>Cad</i>	4	13	2	5	3	MHSP	117	22	9	
	<i>ATLad</i>	15	8	3	3	3	FHSP	117	22	9	

Table 13. Coefficient of Variation (CV) of estimates of BFT-E adult population abundance (biomass of fish of ages 5 and older), obtained with initial sampling scheme for CKMR but halving the sample sizes in Table 4.

<i>CV of estimates by year:</i>										
	2014	2015	2016	2017	2018	2019	2020	2021	2022	
Biomass (5+)	0.68	0.60	0.51	0.43	0.36	0.31	0.27	0.24	0.23	
	2023	2024	2025	2026	2027	2028	2029	2030		
Biomass (5+)	0.22	0.22	0.23	0.24	0.25	0.26	0.27	0.28		

Table 14. Expected number of meaningful kin pairs: (a) POPs, (b) HSPs (MHSPs & FHSPs), obtained with initial sampling scheme for CKMR, under alternative possibilities about population structure.

Population structure	POPs							HSPs (MHSPs & FHSPs)		
	Total POPs	Potential Parent	Potential Offspring					Wlar	CROjuv	CROjuv
			Wlar	CROjuv	Wad	Cad	ATLad	Wlar	Wlar	CROjuv
$pf = 0.9$ $pf1 = 0.9$	473	Wad	164	21	25	7	14	467	89	34
		Cad	15	53	7	21	13			
		ATLad	61	33	13	13	13			
$pf \approx 1$ $pf1 \approx 1$	503	Wad	185	17	38	0	13	544	71	39
		Cad	0	67	0	38	13			
		ATLad	61	33	13	12	13			
$pf \approx 1$ $pf1 \approx 1$ CROjuv pure	520	Wad	185	0	38	0	13	544	0	79
		Cad	0	100	0	38	13			
		ATLad	61	33	13	12	13			
$pf \approx 1$ $pf1 \approx 0$	485	Wad	202	18	14	14	15	611	80	33
		Cad	0	56	11	11	11			
		ATLad	60	33	13	13	13			
$pf \approx 1$ $pf1 \approx 0$ CROjuv pure	495	Wad	202	0	14	14	15	611	0	65
		Cad	0	85	11	11	11			
		ATLad	60	33	13	13	13			
$pf = 0.5$ $pf1 \approx 1$	421	Wad	97	29	14	12	14	268	122	29
		Cad	45	38	12	14	13			
		ATLad	61	33	13	13	13			
$pf \approx 0$ $pf1 \approx 0$	398	Wad	61	33	13	13	13	174	135	26
		Cad	61	33	13	13	13			
		ATLad	61	33	13	13	13			

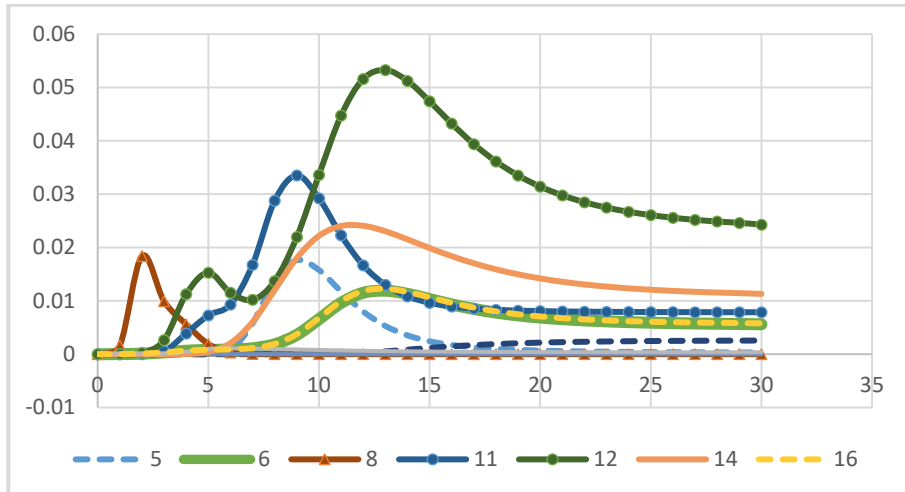


Figure 1. F-at-age by fleet in 2020, as estimated by the 2022 SS3 BFT-E assessment.

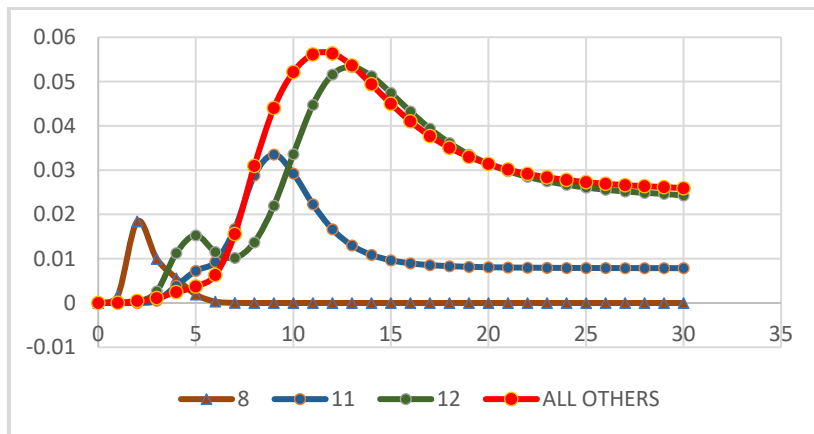


Figure 2. F-at-age by fleet in 2020, as estimated by the 2022 SS3 BFT-E assessment, adding up all non-PS fleets.

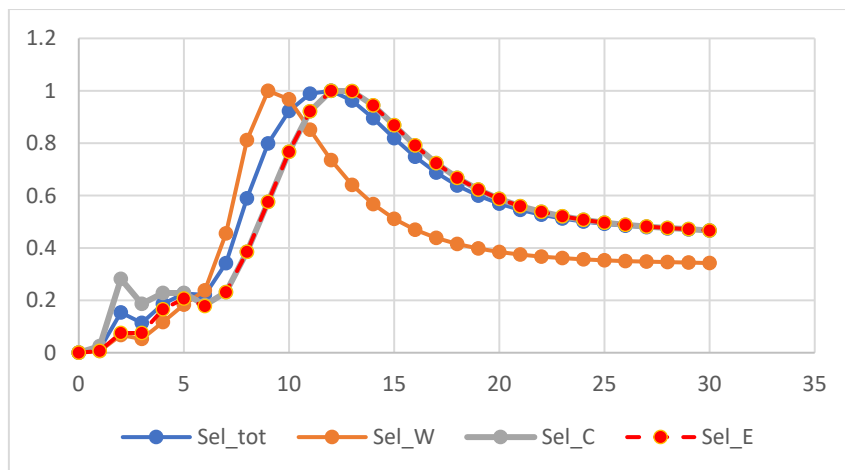


Figure 3. Possible selectivity-at-age per ground (W , C , E), derived to be compatible with the overall selectivity of the 2022 SS3 BFT-E assessment (denoted as Sel_{tot} , in blue).

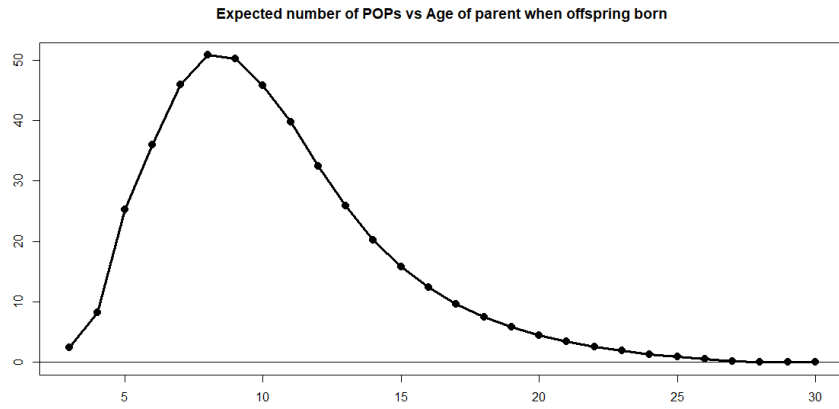


Figure 4. Expected number of POPs versus the age of the parent when the offspring was born, in initial sampling scheme for CKMR.

Qualitative identifiability

One way to answer the question of whether we really can estimate all the spatial-structure parameters (i.e. relating to faithfulness and heritability) is to check numerically whether the Hessian⁸ is positive definite. In this case it is, so in one sense the answer is yes. But (i) that gives no indication of precision (which, for spatial-structure parameters, is likely to vary a lot depending on the true spatial-structure – unlike, say, the precision on total abundance), and (ii) in itself, it does not provide insights as to *why* spatial-structure is estimatable (AKA identifiability).

Previous reports about CKMR for BFT-E have presented a number of schematic arguments around whether/when it is possible to estimate three spawning-site abundances from various combinations of pure, well-mixed, and partly-mixed fisheries. The conclusions were generally encouraging, but rather abstract in the absence of specific proposals for which fisheries to sample. Now that we have specific proposals, it is possible to give a simpler and clearer argument.

The first point to make is that, unless faithfulness is strong, it does not really matter whether we can estimate spawning-site-specific abundances, nor whether initial-spawning-site-choice is heritable or not; the (post-juvenile) fisheries then all operate on all BFT-E. Strong faithfulness alone has management implications but, if in addition strong heritability also occurs, the implications are much greater, because persistently high fishing pressure on one site within the Med could systematically deplete the population associated with that site. In this Appendix, we therefore ignore the not-faithful cases where spatial structure is basically irrelevant, and concentrate first on the faithful/not-heritable case and then on the faithful/heritable case. In order to focus just on the spatial aspects, we deal only with a red-fish/blue-fish cartoon scenario, with no complications of age-structure, no mortality between sampling events, only females considered (so no factors of 2 or 4 in POP probabilities), etc.

Suppose there are N_W, N_C, N_E adults registered at each spawning site, with total $N_+ = N_W + N_C + N_E$. The adult fisheries are either well-mixed (*ATLad*) or pure (*Wad, Cad*). The *Wlar* fishery is pure, and the only partly-mixed fishery is *CROjuv*. Let p_W, p_C, p_E be the weightings of the three N 's offspring in the *CROjuv* samples (which must sum to 1), and write $p^T N = p_W N_W + p_C N_C + p_E N_E$. Overall, we would like to estimate 5 parameters: three N 's and two p 's (only two because of the sum-to-1 constraint).

Starting with POPs, we have the following comparisons available:

ATLad – Wlar and ATLad – CROjuv .

Since the Atlantic fisheries are well-mixed, the empirically-observed POPs-per-comparison rate in these two cases each gives an estimate of N_+ , since

$$\begin{aligned} \mathbb{P}[\text{ATLad-Wlar POP}] &= \frac{N_W}{N_+} \times \frac{1}{N_W} + \frac{(N_C + N_E)}{N_+} \times 0 = \frac{1}{N_+} \\ \mathbb{P}[\text{Atl-CroJuv POP}] &= \\ &= \frac{N_W}{N_+} \times \frac{p_W N_W}{p^T N} \times \frac{1}{N_W} + \frac{N_C}{N_+} \times \frac{p_C N_C}{p^T N} \times \frac{1}{N_C} + \frac{N_E}{N_+} \times \frac{p_E N_E}{p^T N} \times \frac{1}{N_E} \\ &= \frac{p_W N_W + p_C N_C + p_E N_E}{N_+ p^T N} = \frac{1}{N_+} \end{aligned}$$

where the first factor in each product is the probability that the adult sample will be from the spawning ground in question, the second is that the juvenile sample is from the same spawning ground, and the third is all the other adults at that spawning ground that Our adult sample is competing against. Thus we only get one piece of information (albeit a very useful piece) from these two comparisons.

Wad-Wlar

This leads directly to an estimate of N_W , since

$$P[\text{Wad-Wlar POP}] = 1 \times 1 \times \frac{1}{N_W}$$

This is our second piece of information.

⁸ Second derivative matrix of the CK log-likelihood, evaluated at the true (i.e. assumed) parameters

Cad-Wlar

There won't be any of these, assuming faithfulness. (If there are some, it means that $pf < 1$, and the information content of these POPs will be used up in estimating pf .) So this does not provide any extra information on abundance.

Wad-CROjuv

We have:

$$P[\text{Wad-CROjuv POP}] = 1 \times \frac{p_W N_W}{p^\top N} \times \frac{1}{N_W} + 0 + 0 = \frac{p_W}{p^\top N}$$

This is our third piece of information, though it does not have a direct interpretation by itself.

Cad-CROjuv

Similarly to the last case, we have

$$P[\text{Cad-CROjuv POP}] = 0 + 1 \times \frac{p_C N_C}{p^\top N} \times \frac{1}{N_C} + 0 = \frac{p_C}{p^\top N}$$

giving us a fourth piece of information, again without immediate interpretation.

So the POP comparisons give us 4 pieces of information, but we have 5 unknown parameters to estimate. The best place to look is the HSPs from the two juvenile fisheries, Wlar and CROjuv. In this completely-faithful scenario, we will not see Wlar-CROjuv, but we still have two pieces of data: the rate of Wlar-Wlar HSPs, and the rate of CROjuv-CROjuv HSPs. Unfortunately, the absolute number of HSPs is influenced not just by adult abundance, but also by adult age structure (see explanation elsewhere—including numerous previous documents). Therefore we cannot expect those two pieces of data to both provide spatial information, but we can probably use their ratio, since the latter is unaffected by age composition issues (assuming similar age compositions among the three N 's; see below).⁹ Specifically, we have the following, using \propto instead of $=$ to reflect the lack of absolute information:

$$\begin{aligned} P[\text{Wlar-Wlar HSP}] &\propto \frac{1}{N_W} \\ P[\text{CROjuv-CROjuv HSP}] &\propto \frac{p_W N_W}{p^\top N} \times \frac{p_W N_W}{p^\top N} \times \frac{1}{N_W} + \frac{p_C N_C}{p^\top N} \times \frac{p_C N_C}{p^\top N} \times \frac{1}{N_C} + \frac{p_E N_E}{p^\top N} \times \frac{p_E N_E}{p^\top N} \times \frac{1}{N_E} \\ &\propto \frac{(p^2)^\top N}{(p^\top N)^2} \\ \Rightarrow E \left[\frac{\text{rate of CROjuv-CROjuv HSP}}{\text{rate of Wlar-Wlar HSP}} \right] &\approx \frac{N_W \times (p^2)^\top N}{(p^\top N)^2} \end{aligned}$$

This gives the 5th independent piece of information, making it (just) possible to estimate all 5 parameters, and in particular the three N_W, N_C, N_E — even without having any pure E samples. Precision is probably best investigated numerically, but it will certainly depend on the actual values of the p 's as well as the N 's, and the former at least are completely unknown at this point.

The above argument appears to rely on the assumption that adult age structure is amongst the W, C, and E adults. That may not be a good approximation if faithfulness is strong, because the within-Mediterranean fisheries might exert substantially different Z 's on the three quasi-stocks. In practice, though, we would have extra information to help disentangle age-composition effects, in particular on the scale of the fisheries involved (e.g., the total catches from the Wad and Cad fisheries, plus of course their age compositions). Therefore, it seems reasonable to conclude that age-composition effects on HSP probabilities could probably be dealt with inside a model even if age-compositions differ somewhat, so that the assumption may not be as restrictive as it appears.

⁹ For simplicity, we neglect parental mortality here; it does not affect the basic spatial argument, since it can be estimated from a completely different aspect of HSP data, namely the rate-of-change of HSP proportion as a function of inter-birth gap, independently of the overall level of HSPs.

The main complicating factor in this analysis is that the CROjuv fishery is likely to be mixed, and so there are extra parameters to estimate (p). It is therefore reasonable to ask what would happen without CROjuv samples, at least in terms of inference about spatial structure. There are several answers:

- quantitatively, we would not be able to split C and E adults (i.e., we could only estimate $N_C + N_E$, as well as N_W);
- the estimate of Z (which ultimately would come from Wlar-Wlar HSPs) would pertain *only* to W adults;
- qualitatively, there would be less ability to check the well-mixed assumption for Atlantic samples, e.g. by comparing the POP rates where the adults come from one or more the Atl fisheries, and the juveniles from Wlar vs from CROjuv.

The take-home message from all this is that, given adequate samples from the 5 types of fishery considered in this report, it is likely to be possible to estimate site-specific quasi-stock abundances even when faithfulness is high (the most difficult case, and the most important one), including for the E quasi-stock even without any pure samples of juveniles or adults from it. That would not be possible without samples from all 5 fisheries, although an aggregate abundance estimate could still be made using Atlantic adults and either of Wlar or CROjuv; however, the ability to check assumptions and to estimate mortality rates independent of abundance would be much diminished.

Heritability

The above probabilities are unaffected by whether-or-not spawning-sites are heritable. Since the juvenile samples have not had a chance to choose a new one for their own spawning, heritability only affects (and can only be estimated from) adult-adult POP comparisons; for example, we will not see any Cad-Wad POPs if spawning-site is strongly heritable. Adult-adult POPs will be much less common than the POPs and HSPs above which involve juvenile fisheries (see Table 5, etc) so it might take longer to assess heritability than faithfulness. On the other hand, detecting strong heritability may not require a large number of POPs, because seeing (say) 0 Cad-Wad POPs when we would expect just 5 would already constitute strong evidence; in contrast, quantitative estimation of site-specific abundances based on the five types of data above is a more intricate estimation process that is likely to require fairly precise measurements. See Task 4 results in the report.