DELphinus
MOuvements
GEStion

Mai 2025

Cartographier le risque de captures de cétacés à partir des données d'effort de pêche et d'observation à la mer (package analytique R, cartes et manuscrit)

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Site web : https://delmoges.recherche.univ-lr.fr

Livrable

WP concerné : WP3
Responsables du WP : Hélène Peltier (ULR), Laurent Dubroca (Ifremer), Robin Failletaz (Ifremer)

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Titre : Cartographier le risque de captures de cétacés à partir des données d'effort de pêche et d'observation à la mer (package analytique R, cartes et manuscrit)

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Résumé

Depuis les années 1990, la France connaît régulièrement des épisodes de mortalités importantes de dauphins, qui entraînent des pics d'échouages sur le littoral Atlantique en hiver. Depuis 2016, les échouages de petits cétacés dans le golfe de Gascogne présentant des traces de capture, atteignent des niveaux inédits. Si les données scientifiques actuelles permettent d'évaluer globalement le risque induit par ces captures accidentelles pour la conservation de la population de dauphins communs, elles sont toutefois trop lacunaires pour comprendre les déterminants écosystémiques et halieutiques à l'origine de ces captures. En concertation avec l'Office français de la biodiversité, les professionnels de la pêche et l'Etat, La Rochelle Université-CNRS et l'Institut français de recherche pour l'exploitation de la mer (Ifremer) ont construit le projet Delmoges (Delphinus Mouvements Gestion). Il vise, dans un premier temps, à combler ces lacunes en allant chercher des nouvelles données sur les habitats des dauphins, sur leurs interactions trophiques dans l'écosystème et leurs interactions techniques avec les engins de pêche. Ensuite, le projet propose d'intégrer les connaissances sur l'ensemble du socio-écosystème pour envisager une diversité de scénarios de diminution des captures accidentelles incluant des solutions technologiques et, enfin, d'en évaluer les conséquences biologiques et socio-économiques.

Ce livrable est composé de deux parties.
La première partie est un package analytique permettant de mettre en œuvre un flux de travail reproductible afin d'estimer et de cartographier le risque de capture accidentelle d'espèces protégées, dont le dauphin commun. Le package R analytique developpé s'appelle Pelarrp, où les initiales « RRP » signifient « Regularized Regression with Post-stratification ». Le package inclut un ensemble de fonctions et de modèles statistiques pour analyser les données issues des dispositifs ObsMer telles que bancarisées par le SIH. Le package inclut également des fonctions pour étudier la co-occurrence spatiale.
La deuxième partie du livrable est un manuscrit détaillant une analyse exploratoire détaillant les liens existants entre les traits individuels de dauphins capturés accidentellement et les techniques de pêche. Tous les individus au sein d'une population ne sont pas nécessairement exposés au même risque de prise accessoire : chez les dauphins, les juvéniles et les mâles semblent être plus sensibles aux prises accessoires. Pourtant, peu d'études ont investigué comment les caractéristiques individuelles (telles que l'âge, le sexe, la taille corporelle, etc.) corrèlent avec les pratiques de pêche chez ces espèces. En

utilisant les observations françaises de prises accessoires, les déclarations et les bases de données d'échouages, nous avons exploré la vulnérabilité phénotypique aux prises accessoires en corrélant les phénotypes des individus capturés accidentellement avec les caractéristiques des opérations de pêche (y compris les engins de pêche, la taille des mailles, la présence d'un dispositif de dissuasion acoustique, les taxa ciblés et pêchés, et l'effort de pêche). Cette investigation nous a permis de décrire les profils de sensibilité et de vulnérabilité aux prises accessoires. Encore une fois, nous avons trouvé que les mâles et les jeunes individus étaient plus sensibles aux prises accessoires, avec des schémas de sensibilité spatio-temporels. Les individus plus petits semblaient être capturés sur la côte nord de la France et au printemps, et plus de mâles étaient capturés sur la côte sud de la France. Nous avons également trouvé que les dauphins de plus grande taille corporelle étaient plus vulnérables aux chaluts par rapport aux filets maillants. Pour ces derniers, la taille et le poids corporel des marsouins communs capturés accidentellement étaient positivement corrélés avec la taille des mailles. Cibler les soles ou les merlus était également associé à une plus grande taille corporelle des dauphins capturés accidentellement par rapport au ciblage des Sparidés ou des bars. Enfin, nous avons trouvé que des individus plus grands étaient capturés accidentellement en présence d'un dispositif de dissuasion acoustique. Nos résultats suggèrent une sensibilité spécifique à l'âge aux prises accessoires et une vulnérabilité aux techniques de pêche, qui peuvent être dues à des facteurs biologiques tels que le comportement social et le régime alimentaire. Cette étude préconise donc une meilleure prise en compte des schémas spatio-temporels dans la sensibilité des individus aux prises accessoires et des vulnérabilités spécifiques à l'âge ou au sexe à certains profils d'activité de pêche.

Dissémination

Type de livrable : package analytique et manuscrit scientifique (soumis dans Ecological Application)
Public : Oui
Lieux de stockage : site web Delmoges et site web Ifremer

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Table des matières

1 Contexte

1.1 CONTEXTE ENVIRONNEMENTAL ET SCIENTIFIQUE

Ce livrable vise à mettre en œuvre la reproductibilité d'une partie des analyses statistiques réalisées dans le cadre des WP2 (e.g. Authier et al. 2025) et WP3. La reproductibilité est importante pour garantir la qualité des résultats obtenus et permettre des ré-analyses ou de nouvelles analyses avec l'acquisition de nouvelles données.

1.2 ROLE DU LIVRABLE

Le livrable est en deux parties :

- un package à installer et utiliser avec le langage de programmation R (R Core Team 2024).
- un manuscrit détaillant une analyse exploratoire détaillant les liens existants entre les traits individuels de dauphins capturés accidentellement et les techniques de pêche

1.3 STRUCTURE DU DOCUMENT

Ce document détaille les fonctions, données et modèles inclus dans le package. Il fournit également un exemple de code pour une analyse des données OBSCAMe (Vignard et Tachoires, 2023 ; Authier et al. 2024). Il conclut sur des représentations graphiques des évènements de captures lors d'opérations de pêche pour un panel d'engins.
Le manuscrit de publication associé est présenté en annexe.

1.4 ACRONYMES ET ABREVIATIONS

Terme	Explication
RPP	Regularized Regression with Post-stratification[1]
SIH	Système d'Information Halieutique

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[1] https://en.wikipedia.org/wiki/Multilevel_regression_with_poststratification

2 Installation

Le package est compilé en un fichier zip à installer depuis une console R (R Core Team 2024). Il est hébergé à l'adresse suivante :

https://gitlab.univ-lr.fr/pelaverse

Le dépôt associé au package est public (version 1.0.0 du package).

2.1 FONCTIONS

Le package *pelarrp* dans sa version 1.0.0 inclut 22 fonctions documentées, détaillées dans le tableau 1.

Tableau 1 : Fonctions incluses dans package pelarrp v.1.0.0

Nom	WP	Description	Theme	Output
ab_ratio	2	Rapport AB	Co-occurrence	scalaire
centre_of_gravity		Centre de gravité		position
geomedian		Médiane géographique		
gloc		Indice de colocalisation global		scalaire
inertia		Inertie géographique		
schoe		Indice de Schoener		
make_distri		Simuler une distribution	Spatial	Liste avec dataframe et objet sf
make_distri_spf		Simuler une distribution de petits poissons pélagiques		
matern_cov		Covariance Matern		
spheri_cov		Covariance sphérique		
st_chess		Identifier les voisins sur une grille		Liste avec les identifiants du voisinnage
asr		Fonction de lien assymétrique	Calcul	scalaire
compute_sigma		Standardisation pour une variance égale à 1		
design_matrix		Splines de Béziers		Liste avec plusieurs matrices
lower		Borne inférieure d'un intervalle de plus haute		scalaire

		densité pour une distribution a posteriori		
upper		Borne supérieure d'un intervalle de plus haute densité pour une distribution a posteriori		
prepare_data	3	Formattage des données OBSMER ou OBSCAMe	Modélisation	Liste avec 3 dataframes
stan_dataprep		Préparation des données pour modélisation avec Stan		Liste
call_stan		Ajustement d'un modèle Stan		Objet de class stanfit
theta		Extraction des distributions a posteriori des paramètres d'un modèle Stan		Matrice

2.2 DONNEES

Le package *pelarrp* dans sa version 1.0.0 inclut 10 jeux de données documentés, détaillés dans le tableau 2.

Tableau 2 : Jeu de données inclus dans package pelarrp v.1.0.0

Nom	Description	Theme	Output
delmogesGrid	Grille régulière sur le golfe de Gascogne	Spatial	Dataframe pour faire un objet spatial
envGrid	Grille associée au données environnementales env2019		
pelgasGrid	Grille régulière sur le plateau du golfe de Gascogne		
env2019	Données environnementales pour simuler des distributions	Environnement	Dataframe
isobath	Données sur les isobathes dans le golfe de Gascogne		Dataframe pour faire un objet spatial
obscame	Données des évènements de capture de dauphins communs collectées par le	Captures accidentelles	Dataframe

	dispositif OBSCAMe (Vignard & Tachoires, 2023)		
pelgasDdel	Distribution estimée des dauphins communs pendant les campagnes PELGAS	Distribution	
planeSurveys	Données d'observations des dauphins communs dans le golfe de Gascogne (campagnes SAMM et SPEE)		
pp	Données spatialisées de biomasse des petits poissons pélagiques au printemps (campagne PELGAS)		
stanmodelcode	Code	Modélisation	Liste

2.3 MODELES

Le package *pelarrp* dans sa version 1.0.0 inclut 9 modèles codés dans le langage de programmation probabiliste Stan (Carpenter et al. 2017). Ces modèles permettent de mettre en œuvre des régressions multi-niveaux avec régularisation (Authier et al. 2021 ; Rouby et al. 2022). Ces modèles sont détaillés dans le tableau 3.

Tableau 3 : Modèles multiniveaux avec régularisation inclus dans package pelarrp v.1.0.0

Nom	Description	Vraisemblance	Nombre d'années
event_intensity	Estimer le nombre de dauphins moyen par évènement de capture	Negative Binomiale tronquée à 0	> 3
gamma_singleyear	Régression multiniveau and multivariée : analyse jointe des évènements de capture, du temps d'opération de pêche (OP) et du nombre d'OP par marée. La	Evènements : Bernoulli Durée OP : gamma Nb OP : Poisson tronquée à 0	1
logsn_singleyear		Evènements : Bernoulli Durée OP : log-skew-normal Nb OP : Poisson tronquée à 0	
logsn_singleyear_asr		Evènements : Bernoulli avec fonction de lien assymétrique Durée OP : log-skew-normal	

	résolution temporelle est à la semaine.	Nb OP : Poisson tronquée à 0	
weibull_singleyear		Evènements : Bernoulli Durée OP : Weibull Nb OP : Poisson tronquée à 0	
gamma_multiyear		Evènements : Bernoulli Durée OP : gamma Nb OP : Poisson tronquée à 0	> 3
logsn_multiyear		Evènements : Bernoulli Durée OP : log-skew-normal Nb OP : Poisson tronquée à 0	
logsn_multiyear_asr		Evènements : Bernoulli Durée OP : log-skew-normal Nb OP : Poisson tronquée à 0	
weibull_multiyear		Evènements : Bernoulli avec fonction de lien assymétrique Durée OP : log-skew-normal Nb OP : Poisson tronquée à 0	

3 Exemple

Le code R (R Core Team, 2024) ci-dessous illustre l’utilisation du package pour analyser les données OBSCAMe (Vignard et Tachoirs, 2023 ; Authier et al. 2024).

```
##----------------------------------------------------------------------------------------------------------
## SCRIPT : Exemple
##
## Authors : Matthieu Authier
## Last update : 2025-05-25
##
## R version 4.4.1 (2024-06-14 ucrt) -- "Race for Your Life"
## Copyright (C) 2024 The R Foundation for Statistical Computing
## Platform: x86_64-w64-mingw32/x64
##----------------------------------------------------------------------------------------------------------

remotes::install_gitlab(host = "https://gitlab.univ-lr.fr", repo = "pelaverse/pelarrp")

lapply(c("tidyverse", "rstan", "skimr", "pelarrp"), library, character.only = TRUE)

rm(list = ls())

data(obscame)

obscame %>%
  skimr::skim()

obscame %>%
```

```
  group_by(year, area) %>%
  tally()

ices_sub <- c("27.7.e", "27.8.a", "27.8.b")
threshold_duration <- 10 * 24
to_keep <- c("27E5", "27E6",
             "26E5", "26E6",
             "25E5",
             "24E2", "24E3", "24E4", "24E5", "24E6",
             "23E4", "23E5", "23E6", "23E7",
             "22E5", "22E6", "22E7",
             "21E5", "21E6", "21E7", "21E8",
             "20E6", "20E7", "20E8",
             "19E7", "19E8",
             "18E7", "18E8",
             "17E8",
             "16E8",
             "15E8"
             )

### données obscame pour 2022
netdef <- prepare_data(df = obscame %>%
                         filter(rectangle %in% to_keep,
                                year == 2022
                                ) %>%
                         rename(PETS = Delphinus.delphis) %>%
                         mutate(event = ifelse(PETS == 0, 0, 1),
                                foDur = foDur / 60 # convert to hours
                                ),
                       gearID = c("GNS", "GTR"),
                       areaID = ices_sub,
                       durationThreshold = c(0.5, threshold_duration)
                       )

# évènement de by-catch
netdef$op %>%
  filter(event == 1) %>%
  pull(PETS) %>%
  table()

netdef$op %>%
  group_by(PETS, year) %>%
  tally()

# descriptif des données
netdef$op %>%
  group_by(year, week, event) %>%
  tally()

netdef$op %>%
  group_by(targetSpecies, week, event) %>%
  tally()

# préparer les données pour Stan
netstan <- netdef %>%
```

```
  standata_prep()

netstan$Q <- 0.99 # 99th percentile for asymmetric link function

### compilation du model
data("stanmodelcode")
cat(stanmodelcode$logsn_singleyear_asr)

## enable parallelization
options(mc.cores = parallel::detectCores())
## do not re-compile if not needed
rstan_options(auto_write = TRUE)

rpp <- rstan::stan_model(model_code = stanmodelcode$logsn_singleyear_asr,
                         model_name = "Regularized Regression with Post-stratification"
                         )

net_model <- call_stan(standata = netstan,
                       stanmodel = rpp,
                       n_chains = 4,
                       n_iter = 3000,
                       n_warm = 2000,
                       pars = c("intercept", "alpha", "delta", "epsilon", "w", "sigma", "sigma_res", "log_lik", "rho", "overdispersion",
"lambda")
                       )

looic <- loo::loo(loo::extract_log_lik(net_model), save_psis = TRUE)

posterior <- theta(stanfit = net_model,
                   week = 1, # ignored with year = 0
                   year = 0,
                   response = "risk",
                   param = "average",
                   skewlink = list(asymmetry = TRUE,
                                   y_bar = netdef$op %>%
                                     pull(event) %>%
                                     mean(),
                                   Q = 0.99
                                   )
                   )
data.frame(week = 1:53,
           risk = apply(posterior, 2, mean),
           lowerbound = apply(posterior, 2, lower),
           upperbound = apply(posterior, 2, upper)
           ) %>%
  ggplot(aes(x = week, y = risk, ymin = lowerbound, ymax = upperbound)) +
  geom_ribbon(fill = "midnightblue", alpha = 0.3) +
  geom_line(color = "midnightblue") +
  theme_bw()
```

4 Représentation cartographique des captures accidentelles

Les données utilisées dans ce package, et appuyant les résultats des livrables du WP3 sont représentées dans cette section. Pour des raisons de confidentialité et de taille, les jeux de données correspondant n’ont pu être inclus dans le package.

Les cartes synthétisent les informations disponibles sur le golfe de Gascogne, définie par les zones CIEM 27.8.a, 28.7.b, 27.8.c et 27.8.d. Les engins de pêche concernés sont ceux pour lesquels au moins une capture accidentelle de dauphin commun a été observée entre 2005 et 2023. Afin de simplifier la complexité des informations disponibles, elles sont agrégées par engins et années, et concernent uniquement les captures accidentelles de dauphin commun.

Les données d’efforts de pêche sont issues de l’algorithme SACROIS, et les données d’échantillonnages des programmes d’observation ObsMer et de ces déclinaisons (programme d'observation du Parc Naturel Marin d'Iroise, programme DACOR de l'OEC, programme LICADO, programme DolphinFree), et OBSCAMe qui inclue le suivi vidéo embarqué. Ces observations correspondent strictement aux jeux de données utilisées dans les différentes actions concernées par les captures accidentelles sur les dauphins communs en France et en Europe : réponse à la saisine annuelle par IFREMER et La Rochelle Université, et données soumises au groupe de travail européen WGBYC. L’ensemble de ces informations a été décrit et commenté dans les livrables du WP3 : L.3.1.2 pour la description des sources de données, L.3.1.1 pour le détail des flotilles et des captures accidentelles associées, L.3.3.3 pour les paramètres déterminants les captures accidentelles pour les fileyeurs.

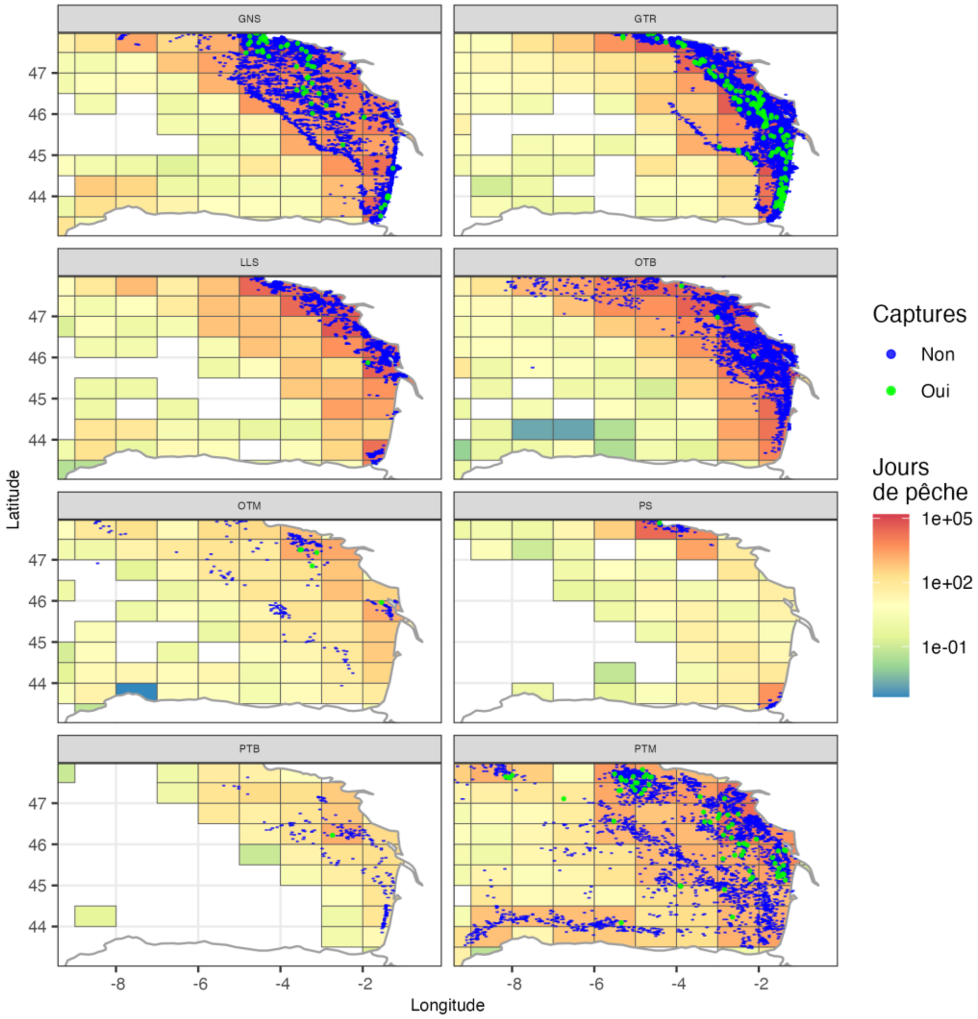

Figure 1 : effort de pêche cumulé (en jour), marées observées (points) avec et sans captures accidentelles par engin de pêche de 2005 à 2023

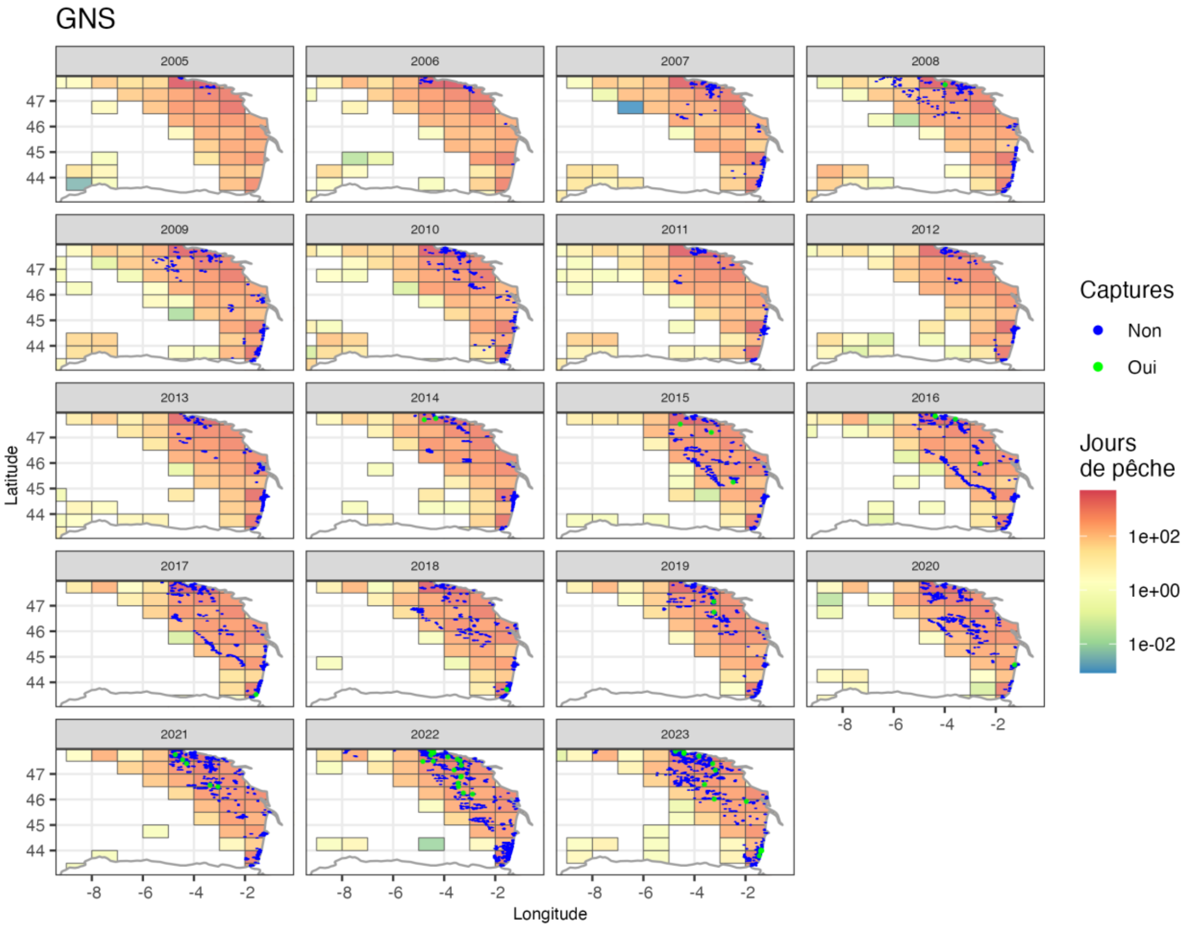

Figure 2 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour filets maillants calés (GNS)

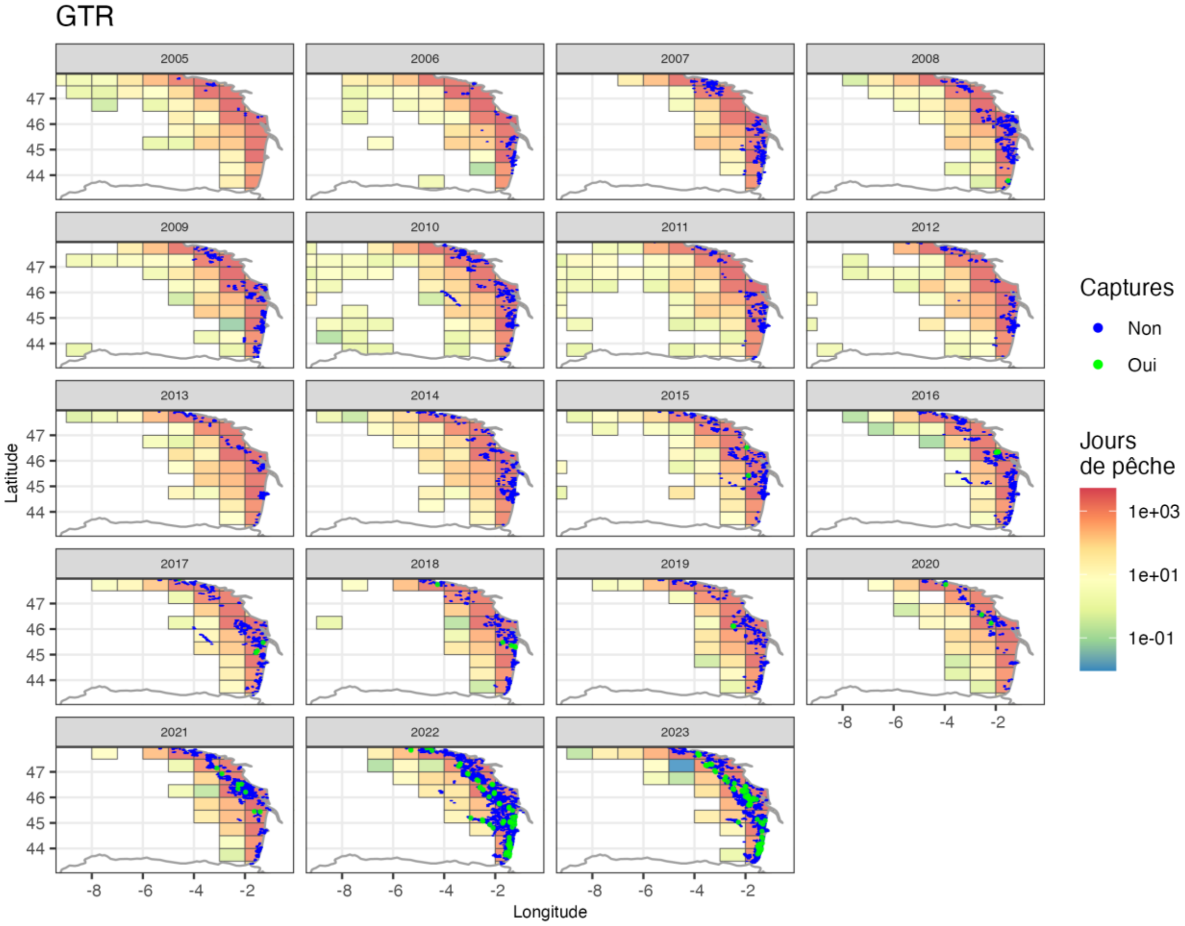

Figure 3 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour trémails (GTR)

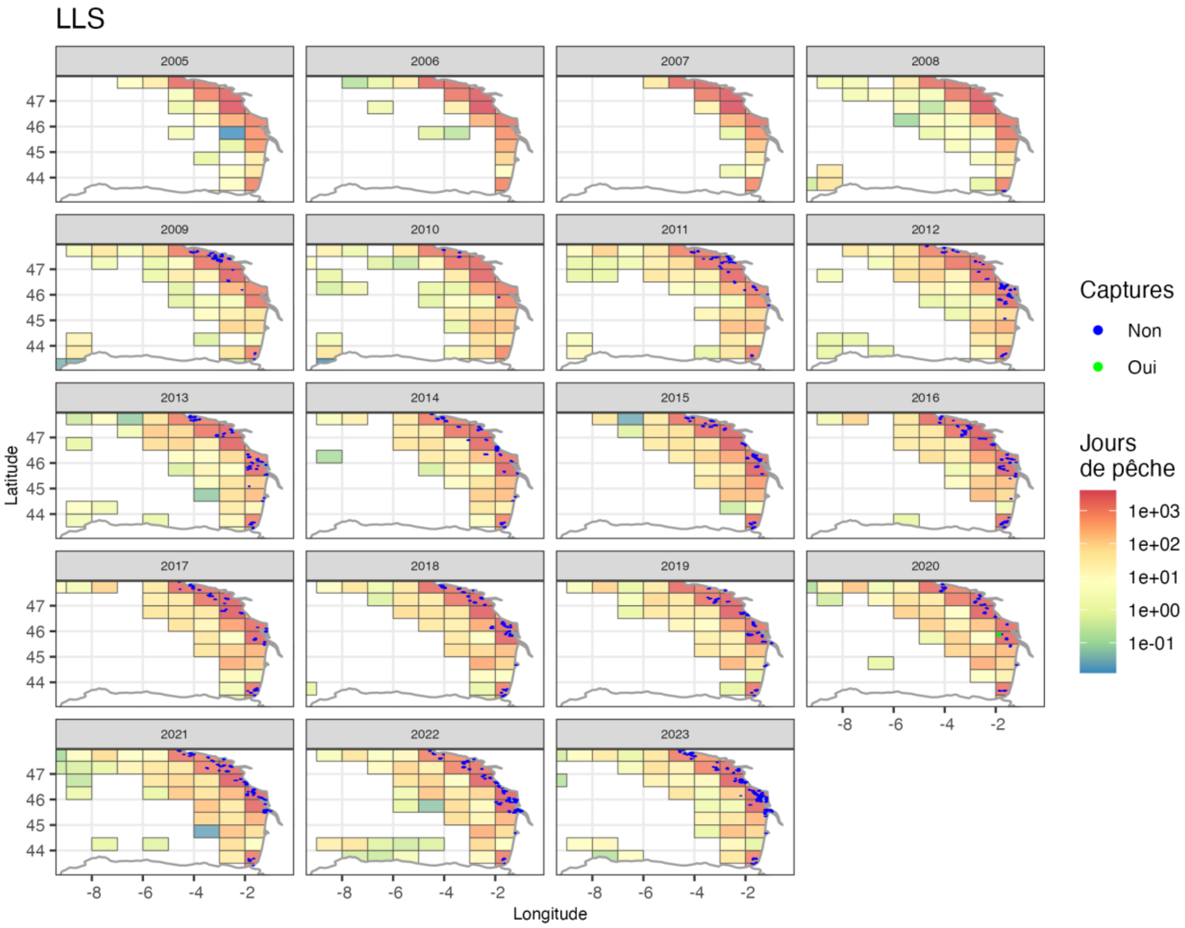

Figure 4 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour palangres calées (LLS)

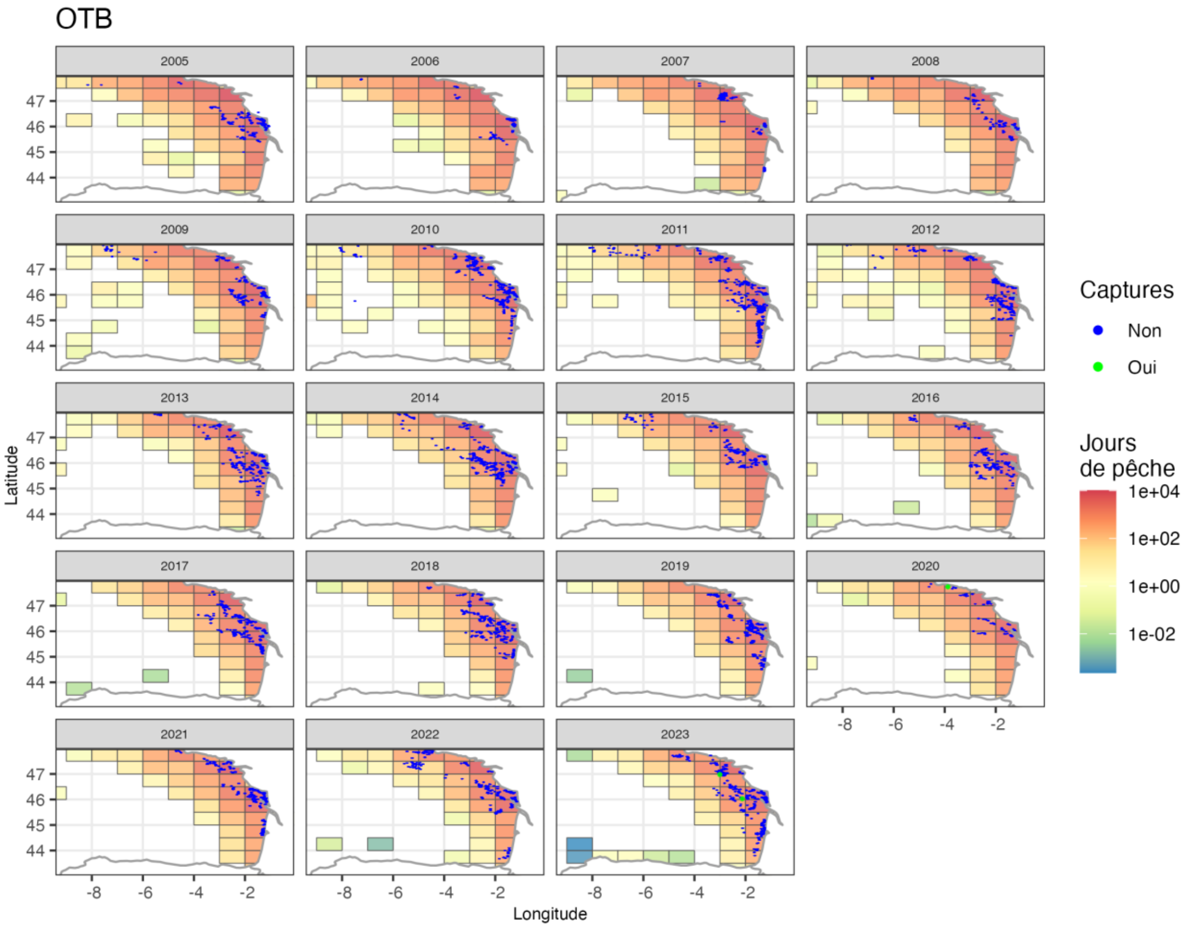

Figure 5 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour chaluts de fond à panneaux (OTB)

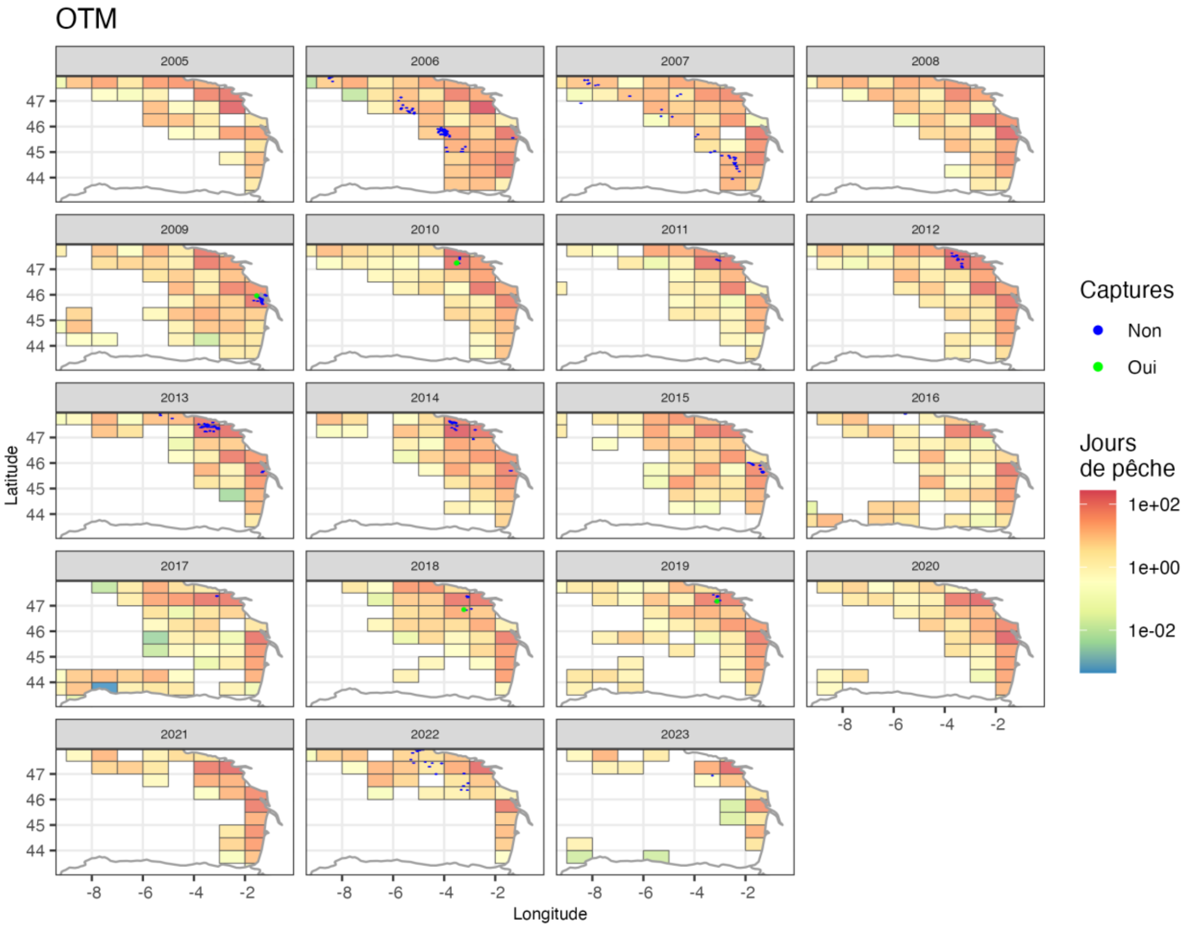

Figure 6 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour chaluts pélagiques à panneaux (OTM)

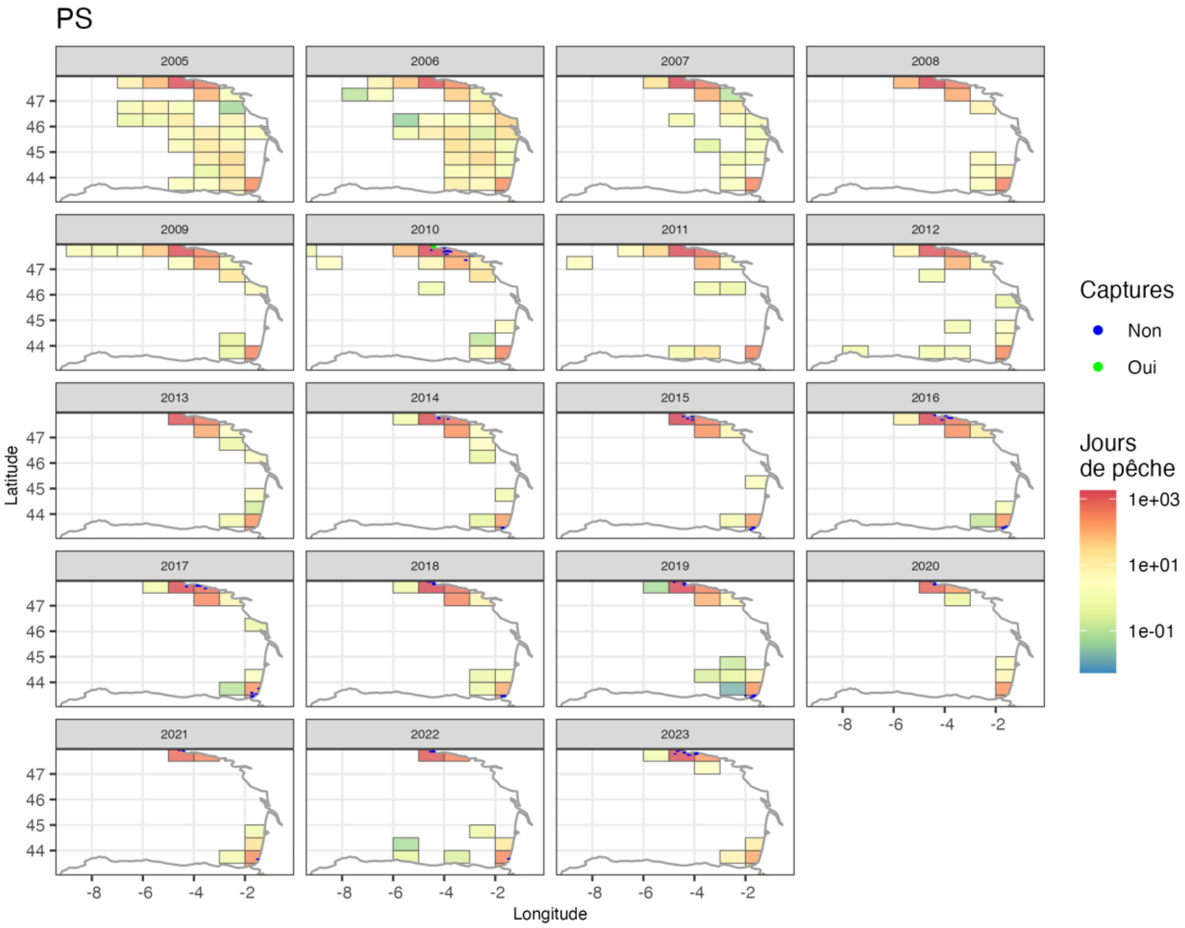

Figure 7 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour sennes coulissantes (PS)

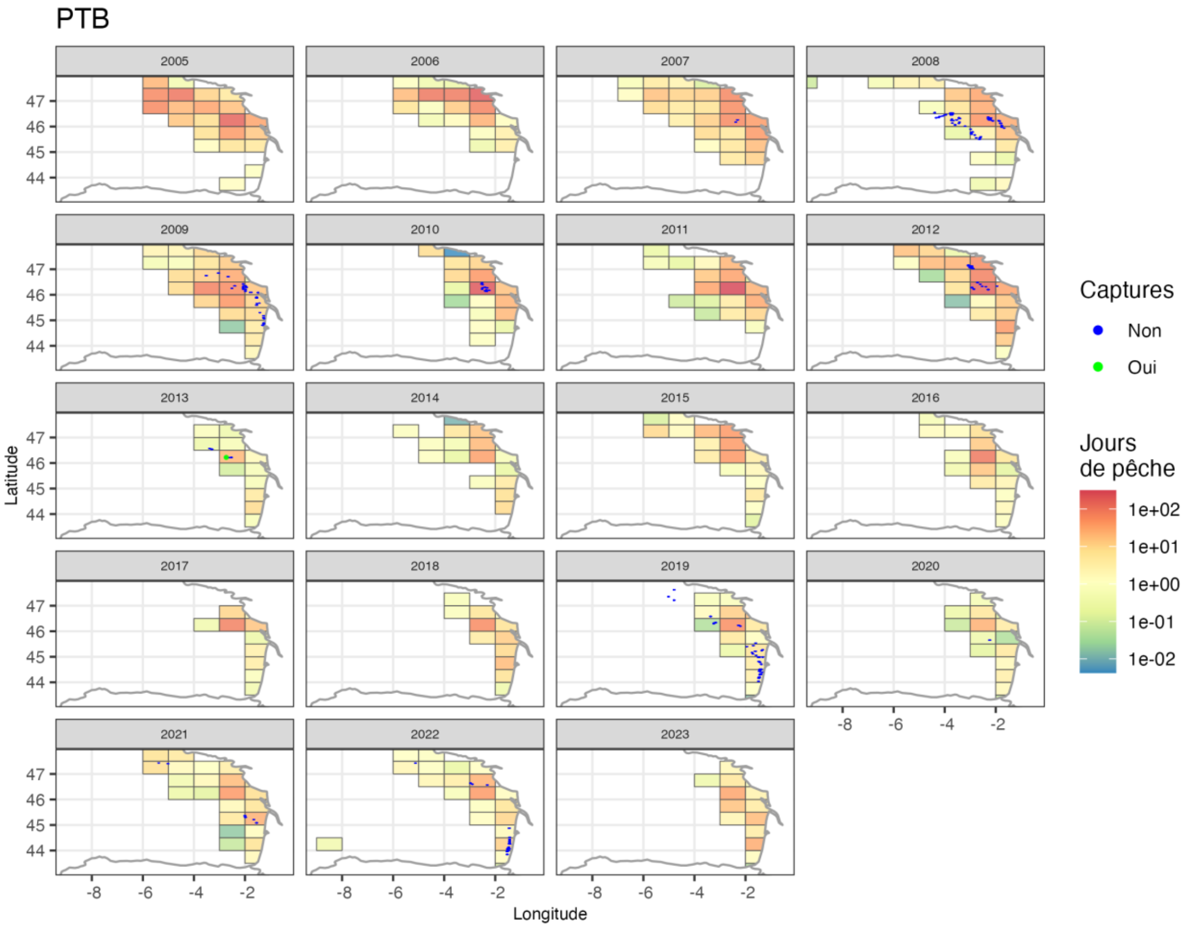

Figure 8 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour chaluts-bœufs de fond (PTB)

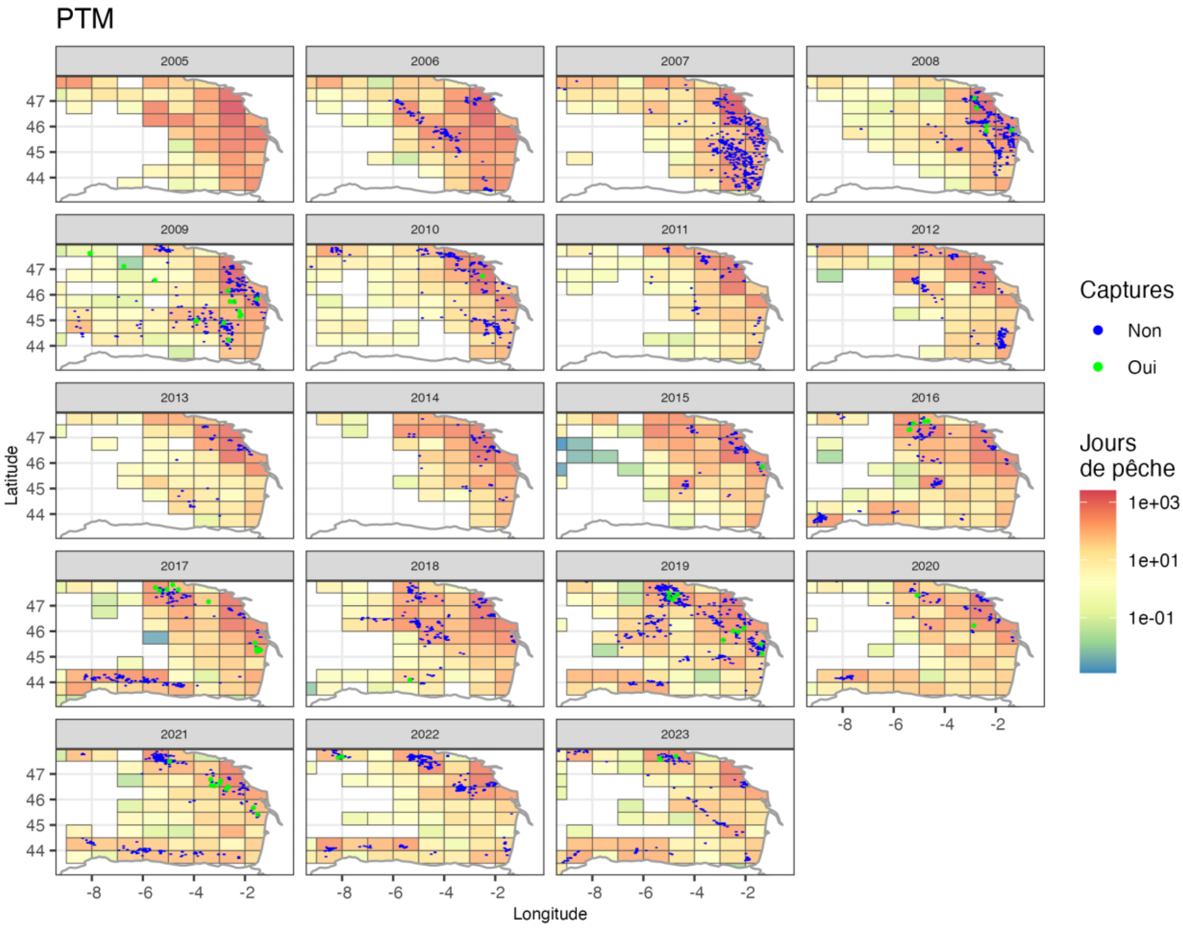

Figure 9 : effort de pêche (en jour), marées observées (points) avec et sans captures accidentelles pour chaluts-bœufs pélagiques (PTM)

5 Bibliographie

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6 Annexe

Annexe 1 : Manuscrit de publication soumis dans la revue « Ecological Application »

Journal: Ecological Applications

Manuscript type: Article

Linking by-caught cetacean traits to fishing techniques: insights from two species of small cetaceans

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Open Research Statement:

Code used to process, analyse the data, and produce the figures and tables of this study is available in Zenodo at https://doi.org/10.5281/zenodo.14810998.

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*Now in UPPA - Université de Pau et des Pays de l'Adour (Avenue de l'Université - BP 576 - 64012 Pau Cedex - France)

Data availability statement:

The fisheries observer data (OBSMER data) and French officially reported by-catch data (SACROIS data) used in this study are owned by the French General Directorate of Maritime Affairs, Fisheries and Aquaculture (DGAMPA: https://www.mer.gouv.fr/peche-et-aquaculture; email: dpma@agriculture.gouv.fr) and are subject to access restrictions. These data are considered sensitive under the General Data Protection Regulation (GDPR) of the European Union (Regulation EU 2016/679), and are not publicly available. However, they can be accessed by qualified researchers upon request through the Fishery Information System at IFREMER, via the following online form: https://sih.ifremer.fr/Donnees/Demande-de-donnees. The specific data query carried out for this study covers the years 2005 to 2023 for OBSMER and 2019 to 2023 for SACROIS.

The stranding data used in this study are owned by the Observatoire PELAGIS - Réseau National Échouage (National Stranding Network), UAR 3462, CNRS-La Rochelle University, and are available upon request (https://www.observatoire-pelagis.cnrs.fr/echouages/reseau-national-echouage/; email: pelagis@univ-lr.fr). The specific data query carried out for this study covers the years 2000 to 2022.

Keywords: Incidental by-catch; *Delphinus delphis*; *Phocoena phocoena*; Fishing behaviours; By-catch risk; Phenotype sensitivity; Phenotype vulnerability; Cetacean conservation; Spatio-temporal management

Abstract

By-catch is one of the main threats currently looming over small cetaceans worldwide. Improving knowledge of the interactions between fishing activities and small cetaceans is paramount to design cost-effective mitigation measures. In particular, not all individuals within a population may be exposed to the same by-catch risk: in dolphins, juveniles and males appear to be more sensitive to by-catch. Yet, few studies have investigated how individual-level characteristics (such as age, sex, body size, etc.) correlate with fishing practices in these species. Using French by-catch observations, declarations and stranding databases on two small cetaceans (*Delphinus delphis* and *Phocoena phocoena*), we explored phenotypic vulnerability to by-catch by correlating the phenotypes of by-caught individuals to fishing-operation characteristics (including fishing gear, mesh size, the presence of an acoustic deterrent, targeted and fished taxa, and fishing effort). This investigation allowed us to outline by-catch sensitivity and vulnerability profiles. Again, we found that males and young individuals were more sensitive to by-catch, with spatio-temporal sensitivity patterns. Smaller individuals appeared to be caught on the northern French coast and in spring, and more males were caught on the southern French coast. We then found larger body-sized dolphins to be more vulnerable to trawls compared to gillnets. For the latter fisheries, the size and body weight of by-caught harbour porpoises were positively correlated with mesh size. Targeting soles or hakes was also associated with a larger body size of by-caught dolphins compared with targeting Sparidae or sea bass. Finally, we found larger individuals to be by-caught in the presence of an acoustic deterrent device. Our results suggest age-specific by-catch sensitivity and vulnerability to fishing techniques, which may be due to biological factors such as social behaviour and diet. Our study therefore advocates for a better consideration of spatio-temporal patterns in individuals' sensitivity to by-catch and age- or

sex-specific vulnerabilities to particular fishing activity profiles.

Introduction

By-catch, the unintentional capture or killing of non-target species in commercial or recreational fisheries, may lead to population declines (Lewison et al. 2004; Soykan et al. 2008). To prevent such declines, it is necessary to implement management measures (Lewison et al. 2004; Komoroske and Lewison 2015; Read 2008). In particular, it is key to assess the impact of by-catch and seek mitigation measures, including technological devices such as acoustic deterrents for marine mammals (*e.g.* Puente et al. 2023). Recent research has made significant progress in quantifying risks (Hines et al. 2020; Mannocci et al. 2021; Zhou et al. 2019) by (i) identifying which practices are the most conducive to by-catch (Clay et al. 2019; Gilman et al. 2016; Peltier et al. 2020; Peltier et al. 2021); by (ii) estimating rates more accurately (Carretta 2021; Kindt-Larsen et al. 2023; Rouby et al. 2022); and by (iii) better understanding exposure within a population (Byrd and Hohn 2017; Gianuca et al. 2017; Heswall et al. 2021). Specifically, in small cetaceans, by-catch phenotypic sensitivity (i.e. likelihood of by-catch as a function of individuals' traits) is often related to sex or age. In common dolphins (*Delphinus delphis*), males are often more prone to by-catch (Fernández-Contreras et al. 2010; López et al. 2002; Westgate and Read 2007; McGovern et al. 2018; but see Meager and Sumpton 2016 in another area), especially young males (Brown, Reid, and Rogan 2014). In bottlenose dolphins (*Tursiops truncatus*), this is the case for juveniles (Byrd and Hohn 2017), and again especially young males (Fruet et al. 2012). High by-catch mortality is also frequently reported in mature females (Brown, Reid, and Rogan 2014 in common dolphins, Fruet et al. 2012 in bottlenose dolphins, Marçalo et al. 2021 in striped dolphins *Stenella coeruleoalba*, Vishnyakova and Gol'din

2015 in harbour porpoises *Phocoena phocoena*), with potentially important impacts on population dynamics (Moore and Read 2008).

Fishing techniques modulate by-catch risk (Brown, Reid, and Rogan 2013; Oliver et al. 2015; Northridge et al. 2017). The importance of assessing the trait-specific (as age, sex, size) impacts of fishing techniques on by-catch risk, hereafter referred to as the phenotypic vulnerability to by-catch, and their effects on population dynamics has long been recognised. For example, M. A. Hall (1996) predicted that some fishing techniques could affect more mature individuals than juveniles and consequently impact population growth. However, to our knowledge, no recent study has examined how individual traits of by-caught individuals might be related to fishing techniques (but see Wallace et al. 2008 for turtles or Jones, Hall, and Potter 2010 for elasmobranchs). There is a particular lack of knowledge for small cetaceans (but see De Boer et al. 2012 for bottlenose dolphins).

Previous studies on traits of by-caught individuals have described various mechanisms linking these traits to the by-catch incidence. First, it is hypothesised that dolphins might be mechanically affected by fishing gear: their body size may determine how they become entangled in nets, with mesh size potentially having a selectivity effect, as suggested by Brown, Reid, and Rogan (2014). Second, their feeding behaviour may influence how they interact with fishing gears (Read et al. 2003; Santana-Garcon et al. 2018) with differential risk depending on the overlap between the diet of targeted species and their diet (Brophy, Murphy, and Rogan 2009; Spitz et al. 2013). Finally, existing sex- or age-specific social segregation patterns (Murphy, Pinn, and Jepson 2013) and related variations in behaviours (such as socialising, resting, spatial behaviour, and foraging; Ball et al. 2017; Castro et al. 2020; Castro et al. 2022) or diet (Murphy, Pinn, and Jepson 2013) may account for differential phenotypic vulnerability to fishing techniques (*e.g.* Vishnyakova and Gol'din 2015). Thus, behavioural differences in habitat use related to the individual's phenotype (*e.g.* nursery habitats, Castro et al. 2020; Castro et al. 2022; or depth-dependent habitat use, Sprogis et al. 2018) could explain trait-specific by-catch risks.

This study investigated (i) the phenotypic sensitivity to by-catch and (ii) the trait-specific vulnerability to different fishing techniques of unintentionally captured individuals from two protected species of small cetaceans. We tested the above expectations and hypotheses from the literature, by (i) examining the spatio-temporal distribution of by-caught individuals' phenotype and (ii) describing existing correlations between phenotypes of by-caught individuals (age, body size) and fishing techniques used. To this end, we used by-catch data from the French observation programme (OBSMER), French declaration data (skipper logbook), and strandings (French stranding network, coordinated by the PELAGIS observatory) in the Northeast Atlantic waters (FAO area 27), between 2000 and 2023.

Materials & Methods

A graphical summary of the analytical framework is included in Appendix (Figure S1) to provide a synthetic overview of the conducted analyses.

Studied species and areas

This study focused on two small cetacean species: the common dolphin (*Delphinus delphis*) and the harbour porpoise (*Phocoena phocoena*). These are the species of greatest local conservation concern, as they are the most frequently by-caught species in the areas studied (ICES 2019, 2020). They were selected on the basis of data availability (number of recorded by-catches with exploitable data on phenotypes; Appendix: Section S1). Only these two species had sufficient sample sizes to conduct robust statistical analyses (individuals with exploitable data on both phenotypes and fishing techniques: N = 366 reported common dolphins and N = 113 reported harbour porpoises, respectively).

Common dolphins are widespread in the Northeast Atlantic, inhabiting the continental shelf year-round (Certain et al. 2008; Certain et al. 2011; Lambert et al. 2018), and oceanic waters in summer (Lambert et al. 2017; Gilles et al. 2023). These dolphins can form large social groups (up to several thousand individuals), with some sex and age segregation, particularly outside the mating period (Murphy, Pinn, and Jepson 2013). The Northeast Atlantic population is estimated to be over 600,000 individuals (ICES 2020). Their primary diet consists of small, fatty fish such as sardines and anchovies (Meynier et al. 2008), but they also prey on Gadiformes species such as hake, whiting and bib in neritic areas (Brophy, Murphy, and Rogan 2009; Santos et al. 2013), as well as Myctophids in oceanic zones (Brophy, Murphy, and Rogan 2009; Spitz et al. 2010).

By-catch is recognised as a major threat to this species (Taylor et al. 2022), with estimates in the Bay of Biscay ranging from 3,650 to 4,700 dolphins per year between 1997 and 2009 (Peltier et al. 2016), and more recent estimates of over 10,000 dolphins caught per year (ICES 2020).

Trammel nets, set gillnets, and pair trawls have been identified as particularly prone to by-catch (ICES 2019, 2020; Peltier et al. 2020; Peltier et al. 2021; De Boer et al. 2012; Fernández-Contreras et al. 2010). Common dolphins are frequently observed interacting with fishing gears, including depredation interactions (*e.g.* Lauriano et al. 2009; Milani et al. 2019 for gillnets; Fertl and Leatherwood 1997; De Boer et al. 2012; Giménez et al. 2021 for trawls).

The harbour porpoise is a common cetacean in the Northeast Atlantic, inhabiting cold temperate and subpolar waters. It is found primarily on continental shelves and in shallow nearshore waters less than 200 metres deep, although it also navigates deeper waters (Bjørge and Tolley 2009; IAMMWG, Camphuysen, and Siemensma 2015; Jefferson and Curry 1994). Harbour porpoises are solitary or occur in small groups of about two individuals (Torres Ortiz et al. 2021). The latest abundance estimate in the Northeast Atlantic is around 400,000 individuals in the summer of 2022 (Gilles et al. 2023). The species primarily feeds on herring, anchovy, sprat, sand eel, cod, and other gadids (Bjørge and Tolley 2009; IAMMWG, Camphuysen, and Siemensma 2015; Santos and Pierce 2003). By-catch is a significant threat to the species (Caswell et al. 1998; IAMMWG, Camphuysen, and Siemensma 2015; ICES 2020; Taylor et al. 2022), particularly in static nets (IAMMWG, Camphuysen, and Siemensma 2015; ICES 2020; Jefferson and Curry 1994). Interactions with fishing gear, particularly depredation, have been observed in both nets (Maeda et al. 2021; Milani et al. 2019) and trawls (Fertl and Leatherwood 1997).

The available by-catch data, as shown in the next section, originated from the activity records of the French fishing fleet and stranding records on the French coasts. The reported by-catch events are mainly from the Bay of Biscay (primarily in the 27.8.a and 27.8.b ICES divisions: Figure S2) and the English Channel (Figure S2). However, we also analysed data from nearby areas with more limited data availability (Figure S2), such as the Celtic Sea (27.8.f, 27.8.g, 27.8.h divisions), South-West Ireland (27.7.j and 27.7.k divisions), and the southern North Sea (27.4.c division). We have provided detailed information on the distribution of by-catches by area and period in the Appendix (Section S2 and Figures S3 to S7).

Data: sources and retained fishing techniques

Here, we selected characteristics of fishing techniques that have been previously identified as high risk of marine mammal by-catch (Brown, Reid, and Rogan 2013; Northridge et al. 2017) and are available in our datasets: fishing gear (gillnet or trawl), mesh size, presence of acoustic deterrents, targeted or fished taxa, and fishing effort (time spent fishing and volume of catch). Data were obtained from three monitoring programmes: direct declaration by fishermen, on-board observations, and stranding observations.

Declaration data

We retrieved by-catch data declared by skippers between 2019 and 2023. These data are available in the SACROIS workflow from the French SIH system ('Système d'Information Halieutique', *i.e.* Fishing Information System; Leblond et al. 2008). The reporting of cetacean by-catch in logbooks has been mandatory in France since 2011, but the related data flow has only been operational since 2019. This dataset contains a large number of by-catch events with exploitable data on by-caught individuals' phenotype (N = 170, both studied species combined). Yet, it provides little information on fishing techniques: information on the fishing gear used (type, mesh size) was provided in most cases, and the targeted taxon was often reported (in ~75% of cases, see Appendix: Section S3). These three variables were retained for use in all analyses using these declaration data.

On-board observation data

We retrieved by-catch observation data from the OBSMER observation programme (https://archimer.ifremer.fr/doc/00774/88640/). This programme relies on the voluntary participation of skippers who agree to carry an observer on board during the entire fishing trip. Data were collected between 2005 and 2023, resulting in a total sample of 309 by-caught individuals with phenotypic measurements for the two studied species. This programme collects a significant amount of information on fishing techniques. It does so by recording onboard information about the caught taxa and their associated weight (see Appendix: Section S3). In addition, skippers were interviewed about the fishing gear used, associated mesh size, fishing gear dimension, depth and speed of fishing gear, targeted taxa, duration of the fishing operation (*i.e.* soaking time), and presence of an acoustic deterrent device. Among these variables, we discarded the fishing gear speed variable as it was only available for trawls. Additionally, we excluded from analyses metrics that were particularly well described by other retained variables (Kruskal-Wallis and Spearman correlation tests with all p-values close to zero, i.e. $< 2.2^{-16}$ in R software). In particular, fishing gear dimension strongly correlated with the type of fishing gear (Kruskal-Wallis chi-squared: 251), targeted taxa (Kruskal-Wallis chi-squared: 227), and mesh size (Spearman's rank correlation rho: 0.53). Fishing gear depth was also well described by the targeted taxa (Kruskal-Wallis chi-squared: 195), and was associated with a significant amount of missing data (14%). Other remaining variables (namely: type of fishing gear, mesh size, most caught taxa, total catch weight, soaking time, and presence of an acoustic deterrent device) were used in all subsequent analyses using observation data only. All records potentially present in both the declaration dataset and the observation programme were discarded from the declaration dataset (as more information is available in the observation dataset; see Appendix: Section S3).

Stranding data

These data are collected daily by the French marine mammal stranding monitoring programme (Réseau national d'échouages, Van Canneyt et al. 2015), coordinated by the Observatoire Pelagis of La Rochelle University (LRUniv). Data spanned from 2000 to 2022 ($N = 3,475$ common dolphins and $N = 871$ harbour porpoises): only stranded individuals with available phenotypic measurements (sex, length, and/or mass) and information on location and carcass decomposition (a proxy for the date of death) were retained for analyses. Stranding reporting rates are stable in France since the 1990s (Authier et al. 2014). We only consider stranded individuals with external evidence of by-catch (as described in Peltier et al. 2020). Note that only a fraction of by-caught individuals are found stranded, as some sink or drift offshore (Peltier et al. 2012).

Data: phenotypic traits and external variables

The three datasets contained information on three by-caught individuals' traits: sex, body mass (BM), and body length (BL). It is important to note that BM is not measured accurately: an "expert opinion" estimate is made *in situ* by the skipper for declarative data, or by observers in the OBSMER and stranding programmes (for the latter, a suspended scale was sometimes used to measure the exact weight where possible). These values were preliminary checked to remove any aberrant estimations (Appendix: Section S1). BL was measured (in cm) with a tape, from the tip of the rostrum to the median notch of the caudal fin. Sex was determined by assessing the presence of mammary slits and the relative position of genital slits and anus, following the method described in Van Canneyt et al. (2015). In declarative data, only BM was available, while the other two datasets contained information on BM and/or BL and/or sex. For individuals with measurements on multiple traits, BM and BL were found to be positively correlated in both species (Spearman correlation test, all p-values< 0.001, respective correlation coefficients of 0.60 for by-caught common dolphin and 0.75 for by-caught harbour porpoise, 0.82 for stranded common dolphin and 0.81 for stranded harbour porpoise), whereas BM and BL of by-caught individuals did not differ significantly between sexes for either species (Wilcoxon tests; for BL: $p= 0.24$ for common dolphin, $p= 0.95$ for harbour porpoise; for BM: $p= 0.92$ for common dolphin, $p= 0.56$ for harbour porpoise). For stranded individuals, BM and BL were significantly different between sexes only for common dolphins (Wilcoxon tests; for BL: $p< 0.001$ for common dolphin, $p= 0.1$ for harbour porpoise; for BM: $p< 0.001$ for common dolphin, $p= 0.76$ for harbour porpoise), but with relatively small differences: males were slightly larger (187 cm ±27 SD, 78 kg ±24 SD) than females (181 cm ±23 SD, 65 kg ±21 SD).

All datasets include information on the ICES division, year, and trimester in which the by-catch occurred. For stranding data, we considered the ICES division where the body was found to be a sufficiently good proxy for the by-catch area of origin. We also considered the trimester and year of stranded individuals by-catch to be those with the greatest overlap with the mortality interval estimate. The observation dataset also includes information on the sea conditions (Douglas sea scale) during fishing operations (trawling or hauling for gillnets) and the time of the day when the operation ended. We used spatio-temporal variables (year, trimester, ICES divisions) to test for potential variation in by-catch phenotypic sensitivity patterns and potential random effects in fishing technique response models (see next section).

Data analyses

We performed statistical analyses and data handling using `R` software (R Development Core Team, 2008, version 4.4.1). We produced graphs with the `ggplot2` package (Wickham 2016).

Phenotypic sensitivity to by-catch

To explore the phenotypic sensitivity to by-catch (i.e. likelihood of by-catch as a function of individuals' traits), we first compared the trait values of by-caught and stranded individuals for each of the species studied with key population values reported in the literature (for both sexes: body length at maturity, asymptotic adult body length; one-sample Wilcoxon tests) and with theoretical equilibrium points (balanced sex ratio; exact binomial tests). The comparisons and the references used to make them are shown in Figure 1 (for both stranding and by-catch data). We then examined whether different phenotypic sensitivity profiles emerged in space or time by implementing a generalised linear model for each of the studied traits (linear model for body length, logistic regression for sex) as a function of year, trimester and ICES division of by-catch. We considered separate body length models for each sex to account for potential sex-specific sensitivity patterns. Implementation of these models was only feasible for stranding data, as the low number of by-catch observations and declarations often resulted in over-parameterised models. Only models on body length were run because this trait was systematically measured for stranded individuals, unlike body mass for which sample sizes were too small (about 92% and 84% of missing values for common dolphins and harbour porpoises, respectively). Body length measurements are also more reliable than body mass in our specific case (body mass values are often guesstimated). We then explored the presence of these spatio-temporal phenotypic profiles by using non-parametric tests (Kruskal-Wallis test for BM and BL, Fisher test for sex), for observed/declared by-catch only. To avoid excessive parameters-to-data ratio, we coded categories to ensure a relative balance with respect to sample size. Thus, for stranding data, we considered periods using four-year group intervals (except for the most recent group, which consisted of the three most recent years). For observed/declared by-catch, data were more fragmented and we therefore grouped close years and ICES divisions into sets of different lengths (see Appendix: Section S4).

Phenotypic vulnerability to different fishing techniques

We then assessed the effect of fishing techniques on by-caught phenotypes (referred to as the phenotypic vulnerability to by-catch) for either species while considering both declaration and observation data sources and the associated described fishing techniques. First, we correlated fishing gear, mesh size, and targeted taxa with 'guesstimated' BM as the response variable: the latter is available in both datasets but has supposedly low accuracy. Then, we only considered the observation dataset, which provides a more detailed description of the fishing techniques used. We tested the effect of various factors, including fishing gear, mesh size, fished taxa, presence of deterrent devices, soaking time, and catch weight, on both BL and sex of by-caught individuals.

We implemented linear regressions for BM and BL models and logistic regressions for sex models. The first step of these analyses involved formatting the explanatory variables used in our models (Appendix: Section S5 and Figures S8, S9, S10). Briefly, we pooled sparse categories where necessary and possible in whole datasets, excluded the rarest categories (or groups of categories) from each data subset used for analyses, removed variables with too much multicollinearity, and tested for the inclusion of potential random effects of spatio-temporal variables (year interval, trimester, ICES division) in the models used.

Model selection and checking

For each model, preliminarily testing of collinearity used the generalised variance inflation factor (GVIF) from the `vif` function in the `car` R package (Fox and Weisberg 2019). More specifically, when models included factor variables with more than two categories, $\mathrm{GVIF}^{1/(2df)}$ was used: a value greater than 2.24 (*i.e.* a GVIF > 5 for one-degree-of-freedom variables) was the cut-off. In such cases, we removed the variable with the highest $\mathrm{GVIF}^{1/(2df)}$ (or GVIF) value. All these values were found to be low enough (≤ 1.05) to run our models on phenotype sensitivity without any correction. We provided GVIF values associated with phenotype vulnerability models in Table S1. For non-parametric tests used in phenotype sensitivity analyses, we checked for collinearity between pairs of variables using Fisher tests.

Significance testing (analysis of variance) used the `car` R package (Fox and Weisberg 2019) (see Tables S2 and S6). Only statistically significant effects at the 5% level were interpreted (Figures 2, 3, 4, and 5). For categorical variables with significant effects, we performed post-hoc pairwise comparison tests using estimated marginal means (the other variables being held at their average values) with the `emmeans` R package (Lenth 2024), using Tukey's correction for multiple testing (Tables S3, S4, S7). In the specific case of logistic regression, the comparison was performed on the log odds ratios (z-tests). For non-parametric tests, we used pairwise Wilcoxon (for BL) or Fisher (for sex) tests (Table S5). We plotted the predicted traits distributions to illustrate the marginal effect of significant variables (all other variables being held at their average values), using the `ggeffects` R package (Lüdecke 2018, `ggeffect` function).

Model fit was assessed using R-squared metrics (Nagelkerke pseudo R-squared for logistic regressions, Nagelkerke 1991), reported in Tables S2 and S6. Compliance with model assumptions was checked graphically using the `DHARMa` R package (Hartig 2022), based on analysis of the distribution of simulated residuals for perfect model fit. When we found a significant deviation from a uniform distribution of simulated residuals (similar to testing for normality of residuals) or between observed and predicted residuals distribution (similar to testing for heteroscedasticity), we applied data transformation to meet expectations (square root and square or cubic transformation for positively and negatively skewed data, respectively). After such transformations, we observed no further deviations from the assumptions. The statistics obtained after variable transformation are shown in Tables S2, S3, S4, S6 and S7. Results were nearly identical before and after transformations. We also assessed the presence of influential values graphically and caveated interpretations accordingly. Plots illustrating effects display untransformed data (see Figure S11 for plots with transformed data).

Results

A synthesis of the main results from the phenotype sensitivity and vulnerability analyses is provided in Table 1, which summarises the main effects observed.

Phenotypic sensitivity to by-catch

In both species, we found more stranded males than females with external evidence of by-catch (exact binomial tests, $p < 0.001$ for both common dolphins and harbour porpoises; Figure 1). Reported by-catches involved about as many males as females, as illustrated by an even sex ratio (exact binomial tests, $p = 1$ for common dolphins, $p = 0.60$ for harbour porpoises). BL of by-caught common dolphins of both sexes was significantly lower than (i) the asymptotic BL (Wilcoxon tests, p-values< 0.001 for males and females, for both strandings and observed/declared by-catch data), and (ii) the BL at sexual maturity (Wilcoxon tests, p-values< 0.001 for males, ≤ 0.017 for females, for both strandings and observed/declared by-catch data). For harbour porpoises, BL of both sexes was smaller than BL at maturity and asymptotic BL only in stranding data (Wilcoxon tests, p-values< 0.004). In contrast, BL did not significantly differ from these values in observed or declared by-catch data (Wilcoxon tests, p-values> 0.05), except males BL that were significantly larger than BL at maturity (p-values< 0.03). There were no statistically significant sex-differences in the weight and size class distributions of by-caught individuals (see Figures S12 and S13 on the two data sources). We provided model results on spatio-temporal sensitivity patterns among stranded individuals in Table S2 and illustrated statistically significant results in Figures 2 and 3 for common dolphin and harbour porpoise, respectively. In common dolphin, more by-caught females were reported in autumn (fourth trimester; Table S3) and in the northern part of the Bay of Biscay (division 27.8.a, especially when compared to the southern division 27.8.b; Table S3). BL of stranded males decreased over the years (except for the period 2004-2007 with particularly small-sized individuals, comparable to the most recent years; Table S4). Average male BL was smaller in spring (second trimester) and then increased with a peak in winter, especially when compared to summer (i.e. first trimester compared to third; Table S4). There was a latitudinal gradient in male BL, increasing towards the south of the distribution (Table S4). Female BL was higher in the Bay of Biscay than in the English Channel (Table S4). In harbour porpoises, as already found in common dolphins, more males were by-caught in the south of the Bay of Biscay (Table S3), with stranded males again being smaller in spring and both males and females being smaller in the northern part of their distribution (particularly in the North Sea, but also when comparing the eastern English Channel with the southern Bay of Biscay; Table S4). Finally, BL of stranded females was smaller between 2012 and 2019, especially when compared to recent years (Table S4).

Looking at spatio-temporal patterns from observed/declared by-catch data (non-parametric tests: Table S5), there were significant period effects in BM of by-caught common dolphins. In contrast to stranding data, BM of by-caught individuals increased in the most recent years (Figure S14). The reported size of by-caught individuals were lower during the second trimester compared to others (Figure S14), a pattern similar to that seen in stranding data. Although not significant, the proportion of by-caught female common dolphins increased in the northern part of the study area (Figure S15), in line with the stranding data.

Phenotypic vulnerability to fishing techniques

Harbour porpoises were primarily by-caught in trammel nets (Figure S8), with a low proportion of reported events also occurring in set gillnets and few reported events in trawls. Reported by-catch events of common dolphins were more evenly distributed between trawls (mainly pelagic pair-trawls) and gillnets (approximately three-quarters in trammel nets and one-quarter in set gillnets). On the other hand, reported by-catch events of harbour porpoises occurred mainly when targeting/catching sole or monkfish (Figures S9 and S10), while those of common dolphins were mainly associated with vessels targeting sole, hake, or sea bass.

Analysis of variance results on how fishing methods correlated with the phenotypic traits of by-caught individuals are provided in Table S6, and statistically significant effects are shown on Figures 4 and 5 for harbour porpoise and common dolphin, respectively. Our analyses of the pooled observation/declaration datasets and the observation data alone showed that BM and BL of by-caught harbour porpoises increased with mesh size. For both common dolphins and harbour porpoises, larger individuals (with higher BL, and also BM for common dolphins only) were by-caught in trawls compared to gillnets. In the case of common dolphins, BM and BL of by-caught individuals were related to the fished/targeted taxa with larger individuals by-caught when fishing/targeting sole and hake (or other Gadiformes) compared to coastal fishes such as Sparidae or sea bass (Table S7; see Figures S9 and S10 for correspondences between targeted/fished ISSCAAP groups and targeted/fished taxa). Targeting Sparidae and sea bass was associated with significantly lower body mass compared to all other targeted species (Table S7). In addition, fishing predominantly for monkfish was associated with smaller BL of by-caught dolphins compared to predominantly fishing for Gadiformes, soles, or sharks and rays (Table S7), the latter being also associated with larger BL than fishing for coastal fishes. Larger common dolphins were also by-caught in the presence of an acoustic deterrent device. Finally, we found the probability of incidentally capturing common dolphin females to increase with the fishing operation's total catch weight (Figure S16). However, this effect was brittle as it hinged strongly on a single by-catch event of 9 females, during a fishing operation associated with the highest total catch weight of the observations ($5,374$ kg, far above other values: $992 \pm 1,462$ SD). Excluding this event, the effect disappeared (p-value = 0.53): we therefore did not interpret it further. No other significant effect of fishing activity metrics on sex was found for either species. Model fits were rather low for all models (Table S6; R^2<0.26), but more especially for models on

BM, using both observation and declaration data (R^2<0.13).

Discussion

Different sensitivity and vulnerability profiles to by-catch ?

Phenotypic sensitivity to by-catch

This study revealed that common dolphins and harbour porpoises by-caught in fisheries flying the French flag and operating in the Northeast Atlantic (for observed/declared data) or active in an area relatively close to the French coast (for stranding data) represent a specific subset of their populations. By-caught common dolphins were significantly smaller than the mean body length of sexually mature individuals or the asymptotic body length of adult individuals. Similarly, stranded harbour porpoises were significantly smaller than the asymptotic body length of adult individuals. This suggests that a large part of incidental catches involve young individuals and mostly immature individuals in common dolphins; a result consistent with other studies such as Murphy and Rogan (2006), Brown, Reid, and Rogan (2014), and Mannocci et al. (2012) in common dolphins or Brennecke et al. (2021) and Torres-Pereira et al. (2023) in harbour porpoises. For stranded individuals only, we also found more males being by-caught than females, for both species. Male-biased sensitivity to by-catch has been frequently described in common dolphins (Brown, Reid, and Rogan 2014; Fernández-Contreras et al. 2010; López et al. 2002; Westgate and Read 2007; McGovern et al. 2018) and also mentioned in harbour porpoises (Torres-Pereira et al. 2023). Differential sex- and size-specific sensitivity to by-catch can result from several non-exclusive factors (Brown, Reid, and Rogan 2014): it could reflect the sex/age structure of the global population, spatial or temporal sex/age segregation (distribution of juveniles or males potentially overlapping areas and periods of high-risk fishing fleet activity), or specific sex- or age-related behaviours leading to differential sensitivity to by-catch. Juveniles, potentially inexperienced, could engage in riskier interactions with fishing gear or lack physical/acoustic skills to avoid entanglement; males could generally take more risks as observed in other mammalian species. On the other hand, we did not find any significant imbalance in the sex ratio reported from observation/declaration pooled data. Moreover, the size of by-caught harbour porpoises in these data did not significantly differ from the asymptotic length of adult individuals and, for males, was even larger than that of mature individuals. These differences with stranding data may emerge from the low sample size available from observation/declaration data, or sex- and age-specific patterns in strandings or in the collection of observation/declaration data (*e.g.* differences in buoyancy, changes in fishermen's behaviour during surveys, under-reporting of specific events).

Trait-specific vulnerabilities to fishing techniques

The reported body length and mass of by-caught individuals also depended on fishing techniques. First, for harbour porpoises only, the body size and mass of by-caught individuals were positively correlated with mesh size suggesting a differential selectivity with larger mesh sizes mechanically increasing the likelihood of by-catching larger porpoises. This results is consistent with the hypothesis raised (but not tested) in Brown, Reid, and Rogan (2014) that mesh size likely contribute to porpoise selectivity. As in this later study, we could draw a parallel with a case study on sharks (McAuley, Simpfendorfer, and Wright 2007), with a similar relationship between the mesh size used and the size of sharks caught. Of note, in the case of the body mass model (and to a lesser extent for the body length model), mesh size is closely linked to targeted taxa: large mesh sizes (greater than 200 mm) are mainly used to target monkfish and only occasionally to target skates and flat fishes. The effect we evidence could then also be linked to potential overlap in the diet of adult harbour porpoises (Santos and Pierce 2003) and monkfish (Fariña et al. 2008) and/or to specific strategies associated with monkfish fisheries (*e.g.* several days soaking time and deeper set: Bjørge, Skern-Mauritzen, and Rossman 2013), which may pose a greater threat to adults as they are known to forage in more offshore areas (Santos and Pierce 2003).

For both harbour porpoises and common dolphins, we also found an effect of fishing gear type on the reported body size, with larger individuals by-caught in trawls than in gillnets. Such a difference between fishing gear types has already been discussed in De Boer et al. (2012) for common dolphins, who argued for a higher vulnerability of calves and juveniles to gillnet by-catch and of mature individuals to trawl by-catch from the overlaps in the distribution of fisheries and age classes. Such a difference is indeed likely to be related to the age of the individuals, with younger (*i.e.* smaller) individuals probably interacting with fishing gears differently than adults. The detection ability of the net could be lower for younger individuals who acquire their echolocation skills during the first year of life, as was evidenced in bottlenose dolphin (Harder et al. 2016). As hypothesised by Murphy and Rogan 2006; Murphy, Pinn, and Jepson 2013, juveniles could also lack experience in interacting with fishing gears. For example, social learning, including foraging strategies, is developed during the first years of life (Kuczaj II, Yeater, and Highfill 2012). Differential age-vulnerability to by-catch in trawls could then result from older individuals taking more risks by learning foraging techniques near or even within the trawl. This was hypothesised by Murphy, Pinn, and Jepson (2013) with the specific example of the pelagic trawl fishery for sea bass and observed in bottlenose dolphins (Santana-Garcon et al. 2018). Finally, differences in the size of by-caught individuals could also results from differential catchability with smaller individuals escaping trawls more easily although there is currently no published evidence.

Only in common dolphins was the size of by-caught individuals larger in the presence of an acoustic deterrent device. This suggests that adult individuals may be more habituated to the presence of acoustic deterrents than juveniles. This habituation has been demonstrated in harbour porpoises (Carlström, Berggren, and Tregenza 2009; Dawson, Read, and Slooten 1998; Cox et al. 2001), but only for short periods. There is currently no similar evidence in common dolphins (Carretta and Barlow 2011). Adult individuals might even be lured by such an acoustic device acting as a 'dinner bell' as observed in pinnipeds (Dawson et al. 2013). Such a behaviour would be consistent with potential depredation occurring for the species studied, as suggested by multiple reports of feeding associated with trawling in the species studied (Fertl and Leatherwood 1997; Gonzalvo and Carpentieri 2023).

Finally, we found that larger common dolphins were by-caught when targeting/fishing Pleuronectiformes (mainly soles) and Gadiformes (mainly hake) compared to coastal fishes (mainly sea bass and sea bream). This could be due to existing age-related differences in diet (Murphy, Pinn, and Jepson 2013): adult males prey on larger and less diverse prey, with a particularly low proportion of cephalopods; relative to females and immatures whose diet is more diverse with, in particular, a high proportion of blue whiting preyed upon by immature males (Stockin et al. 2023). However, these known intra-specific differences in diet are not particularly consistent with our results, suggesting that other mechanisms may be at play. A likely hypothesis is that the differences in by-caught individuals' size as a function of targeted/fished species are due to the overlap between the habitat or diet of these species and the age-specific habitat or diet of dolphins. Indeed, neither sea bream, nor sea bass, nor sole are preyed upon by common dolphins. For the first two, there is likely to be an overlap in diet (Spitz et al. 2013), but also a spatial overlap with the dolphin nursery habitat, as groups of juveniles are more likely to be distributed inshore than adult groups (Cañadas and Hammond 2008; De Boer et al. 2012). In this particular case, there is also likely to be greater overlap with the diet of younger individuals, as the size of prey consumed by these coastal fishes is likely closer to the size of prey consumed by juveniles than adults. Similarly, the by-catch of older dolphins when targeting soles may be due to their co-occurrence in the same habitats at specific periods. For example, dolphins may follow their preferred prey close to the seabed by following their diel vertical distribution (*e.g.* vertical movements of anchovy with a descending phase occurring during the day: Tsagarakis et al. 2012, or sardines with a descending phase during the night: Giannoulaki, Machias, and Tsimenides 1999; Zwolinski et al. 2007). These particular foraging behaviours might be more common in adults than in juveniles, explaining such differences in the size of individuals caught. Hake is the only species of interest that is preyed upon by common dolphins; it is possible that this species is preferentially preyed upon by adult individuals or that the strong overlap with the diet of adult individuals (Cabral and Murta 2002), combined with its more offshore distribution and larger size than coastal fishes, explains that adult individuals are more frequently associated with it. More puzzling are the differences in the size and weight of by-caught individuals observed when fishing for various demersal fish (John Dory, monkfish), but it should be noted that effects of this latter category are supported by fewer data points (Figure 5) and may be brittle. Interestingly, we again observed a strong positive correlation between mesh size and targeted taxa in the declaration dataset (all high mesh sizes are associated with monkfish fishing, similar to what we observed in harbour porpoise). This could explain the prediction of capturing individuals with larger BM when fishing for demersal fish (with an underlying mechanical effect of mesh size, as discussed above for harbour porpoise).

Conservation and management implications

Towards spatio-temporally integrated management

The present results have strong implications for conservation. First, the fact that age and sex classes are not equally sensitive to by-catch may have implications for population dynamics (as observed for albatrosses in Tuck et al. 2015 or hypothesised for common dolphins in Brown, Reid, and Rogan 2014). In our particular case, young individuals appeared to be generally more sensitive to by-catch, except for mature harbour porpoise males, who were also potentially at risk. In both cases, such dynamics could strongly influence the recruitment of the population (by removing individuals before they have reproduced or by reducing the number of potential reproducers) and lead to a declining population (Caley et al. 1996; Horning and Mellish 2012; Wade, Reeves, and Mesnick 2012).

Our study focused on how by-catch risk varies with fishing methods and exogeneous covariates (spatio-temporal variables). In particular, it highlighted that some practices are likely to pose a significant threat to specific age classes. For example, juveniles of both species appear to be particularly vulnerable to gillnet fishing, while juvenile harbour porpoises are also vulnerable to small mesh sizes and juvenile common dolphins to the targeting of coastal fishes. Such results should encourage consideration of these parameters when fishing in high-risk environments and periods where juveniles are likely to be present, such as nursery habitats, and may argue for the protection of such habitats (Gilman et al. 2023).

In addition to the importance of fishing techniques in by-catch risk, we also found that spatio-temporal variables often correlated with different patterns in by-caught phenotypes (as also observed for example in López et al. 2002). First, we found that, in both species, smaller males were by-caught in spring (second trimester), with the size of by-caught males gradually increasing afterwards. This may reflect the reproductive cycle of the species, with parturition occurring between April and September for common dolphins (Murphy, Pinn, and Jepson 2013) and between May and August for harbour porpoises (Lockyer 2003). This pattern may be related to the potentially higher risk-taking of young, inexperienced males compared to other sex/age classes. For common dolphins, more females were also by-caught during autumn (fourth trimester), again possibly related to the reproductive cycle: female risk-taking may be higher during lactation, rearing young, or rebuilding reserves with vigilance and foraging behaviours changing after birth, as observed for bottlenose dolphins (Hill, Carder, and Ridgway 2008; Miketa et al. 2018). On the other hand, it could also be related to a higher foraging rate of females after late infancy, as observed in bottlenose dolphins (Krzyszczyk et al. 2017). Second, we found that larger individuals were by-caught in the southern part of the Bay of Biscay than in the northern one, with significantly more males in the southernmost part. This could, again, be related to the reproductive habits of both species with a preference for shallower waters (as can be found in the Channel) as nursery habitat (Koschinski 2001; Spyrakos et al. 2011); and potential spatial age segregation with mature males potentially occupying the southern part of the distribution in a similar vein as the potential segregation between offshore and inshore areas as suggested by Murphy, Pinn, and Jepson (2013). However, it could also be due to differences in the spatial distribution of body size, particularly for harbour porpoises, where such differences have already been described (Murphy et al. 2020), in contrast to common dolphins, for which only a slight size cline has been identified (Murphy, Pinn, and Jepson 2013). On a larger temporal scale, we also found that the size of by-caught male common dolphins or female harbour porpoises tended to decrease over the years. That suggests either an increase in by-catch of young individuals of these sexes, which could be due to a change in the behaviour of these age- and sex-classes; or a change in fishing practices with specific age or sex-related risk pattern; or a depletion of adults and an influx of younger ones, potentially resulting from by-catch dynamics with fewer individuals reaching adult age over the years and demographic compensation through migration or birth rate. These trends again support the implementation of specific measures during periods and in areas of particular risk, for example by enforcing protected areas or temporary closures during key breeding periods and areas (as also suggested by Tuck et al. 2015; Vishnyakova and Gol'din 2015), such as during parturition periods or in potential nursery areas, or by promoting a shift in the fishing effort towards the use of fishing gears with a low risk of by-catch (*e.g.* Jenkins and Garrison 2013).

These preliminary results also argue for better consideration of the risk landscape that emerges from the global environmental context (Gilman et al. 2023). Here, we did not consider exogeneous variables other than spatio-temporal ones known to be important for marine mammal by-catch (Northridge et al. 2017). This choice was partly out of necessity due to missing data and multicollinearity. The two latter points to the need for better study design and sampling in order to fill the gaps and break collinearity patterns arising in part from lack of control over sampling (*e.g.* declared data, voluntary schemes for onboard observers). However, variables such as sea state may be important to the dynamics of by-catch (Northridge et al. 2017; see also Figure S7). In observer data, sea state significantly correlated with sex (p=0.005, Fisher test) and size (p=0.001, Kruskal-Wallis test) of by-caught common dolphins, for example. More males and larger individuals were by-caught during calm sea conditions than during rough sea conditions (Figure S17). This suggests that individuals may behave differently as a function of sea state, age, and sex, with potentially different risk-taking or detection patterns in the vicinity of fishing gear. Such assumptions needs to be confirmed by analyses in that test for an effect of these conditions is independent of the other factors influencing by-catch. In our study, trimester and spatial areas strongly correlated with sea conditions: calm sea conditions were mostly reported in the Bay of

Biscay and rough sea conditions mainly in the Channel Sea; the latter two conditions were also mostly reported in winter (i.e. first trimester). Several other ecological factors have been found to correlate with by-catch risk (see Northridge et al. 2017 for a review): tidal state (Brennecke et al. 2021) or depth (Bjørge, Skern-Mauritzen, and Rossman 2013) for harbour porpoise; light conditions (Du Fresne 2007; see also Figure S6) or depth (Du Fresne 2007; Brown, Reid, and Rogan 2014; Puente et al. 2023) for common dolphins. Other environmental parameters have also been found to be of primary importance in other species, such as turbidity for seals (Luck et al. 2020); or the level of competition in the environment for seabirds (Zhou and Brothers 2021, 2022); or even the facilitation of by-catch by other species such as diving birds bringing bait to the surface, which then affects other seabird species (Jiménez et al. 2012). These variables may also influence the phenotypic profile of by-caught individuals: for example, in our studied species, sex and age segregation profiles as a function of depth have been observed (Murphy, Pinn, and Jepson 2013; A. M. Hall 2011; Smith and Gaskin 1983), and may lead to differential phenotypic sensitivity and/or vulnerability to by-catch.

Finding trade-offs in data collection and management

This study highlights the need to better consider phenotypic data when collecting by-catch information. Echoing Gianuca et al. (2017), we recommend that information on sex and age (or at least their proxies, such as size or weight) should be systematically reported when monitoring by-catch of small cetaceans. In our specific case, these data were systematically collected during the observation programme and stranding monitoring, but information on body mass was often missing from the declaration dataset, which also lacked information on the size and sex of by-caught individuals (completely missing). While measuring size may be time-consuming and may not be adopted by the fishermen, we believe that rapid onboard sex determination should be feasible and should be encouraged (*e.g.* by training). Furthermore, this study shows that rapid onboard estimates may be a good compromise when precise measurements are not feasible or well accepted by the profession. Indeed, models using 'guesstimated' body mass gave results very close to those obtained using precisely measured body size, for variables present in both types of model (see effects of mesh size in Figure 4, or fishing gear type and fished/targeted taxa in Figure 5). This should not mean that precise measurements are not necessary, but rather that fishermen may have a limited time budget for scientific measurements.

Another recommendation would be to be as precise as possible about the context in which by-catches occurred, by providing information on the fishing techniques used and, where possible, the environmental context associated with them. In our particular context, the declaration data are lacking in details, with missing data on the targeted taxa, as well as a general lack of information on the fishing effort and the specificity of the fishing gear (depth, speed) associated with the fishing event. The reporting of such information when by-catches occur should be encouraged to improve the description of the processes involved. Attention should also be paid to the correlation structure of the data collected in the surveys: the areas, periods, and fleets sampled should be sufficiently diverse to represent the existing diversity of practices. The scope for selection bias is large in both the collected declaration and observation data on small cetacean by-catch. Implementing a statistically-driven design (that is, random allocation of observers to fishing trips) instead of leaving it to the discretion of skippers would allow the collection of data that are representative. Currently, representativeness is not guaranteed, and consequently a robust assessment of the causal effects of several variables is not possible.

Studies disentangling the dynamics of bycatch risk should also benefit from improved sampling coverage. Most current sampling methods, such as those used in this research, have major limitations in data collection. Observer programmes often lack coverage due to the high cost of implementation (Babcock, Pikitch, and Hudson 2003), fishermen's declarations are often incomplete (Basran and Sigurðsson 2021), and stranding data do not include all individuals that sink or drift offshore (Peltier et al. 2012). Additional efforts should be made to improve data completeness: increased participation of fishermen in catch reporting (Brevé et al. 2024) and the use of on-board cameras (remote electronic monitoring, Pierre et al. 2024) are probably the most effective and promising solutions.

Lastly, we also recommend that the different species at risk of by-catch be investigated separately, as by-catch phenotypic sensitivity and/or vulnerability could strongly differ between them. We showed how the by-catch risk of the two species differed with respect to fishing techniques, phenotypes, and their interactions. Taking into account these interactions can improve conservation measures (Grantham, Petersen, and Possingham 2008; Gilman et al. 2019). However, we should be cautious to consider all species at risk of by-catch when implementing measures to avoid imposing changes beneficial for one species but detrimental for others (as discussed in Komoroske and Lewison 2015; Gilman et al. 2019). For example, we evidenced that common dolphins and harbour porpoises were caught in different fishing contexts. Reported common dolphin by-catch was mainly associated with pelagic pair trawls, trammel nets, and set gillnets and with vessels targeting either soles, hake or sea bass; whereas reported harbour porpoise by-catch was mainly associated with trammel nets and with vessels targeting mainly either soles or monkfish. Thus, a shift in fishing efforts towards trammel nets targeting monkfish to mitigate common dolphin by-catch could be highly detrimental to harbour porpoises, which are particularly vulnerable to by-catch in these fisheries. Finally, interactions between species of conservation concern when implementing protection measures require also attention as these interspecific interactions can have major effects on population dynamics (Hollowed et al. 2000; Kanaji et al. 2021). Consequently, it is of significant interest to examine the profiles of phenotypic sensitivity and vulnerability to by-catch in multiple species concurrently, in order to understand the implications this could have on their interactions, particularly if these interactions are phenotype-dependent.

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Author Contributions

M. Brevet conceived the ideas and designed methodology; L. Dubroca, H. Peltier and M. Authier collected the data; M. Brevet analysed the data; M. Brevet led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

The authors have no conflict of interest to declare.

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Tables

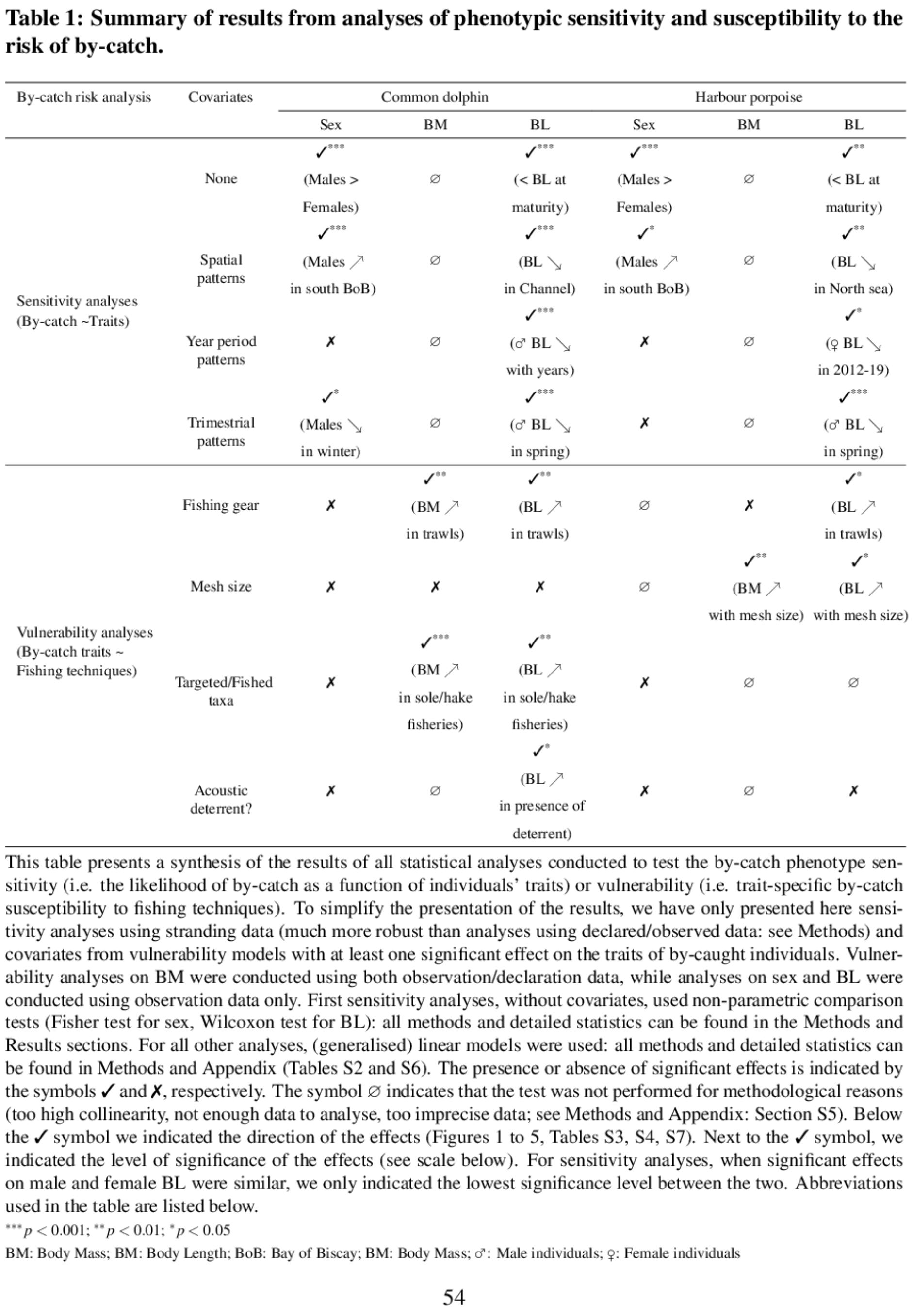


Table 1: Summary of results from analyses of phenotypic sensitivity and susceptibility to the risk of by-catch.

By-catch risk analysis	Covariates	Common dolphin			Harbour porpoise		
		Sex	BM	BL	Sex	BM	BL
Sensitivity analyses (By-catch ~Traits)	None	✓*** (Males > Females)	∅	✓*** (< BL at maturity)	✓*** (Males > Females)	∅	✓** (< BL at maturity)
	Spatial patterns	✓*** (Males ↗ in south BoB)	∅	✓*** (BL ↘ in Channel)	✓* (Males ↗ in south BoB)	∅	✓** (BL ↘ in North sea)
	Year period patterns	✗	∅	✓*** (♂ BL ↘ with years)	✗	∅	✓* (♀ BL ↘ in 2012-19)
	Trimestrial patterns	✓* (Males ↘ in winter)	∅	✓*** (♂ BL ↘ in spring)	✗	∅	✓*** (♂ BL ↘ in spring)
Vulnerability analyses (By-catch traits ~ Fishing techniques)	Fishing gear	✗	✓** (BM ↗ in trawls)	✓** (BL ↗ in trawls)	∅	✗	✓* (BL ↗ in trawls)
	Mesh size	✗	✗	✗	∅	✓** (BM ↗ with mesh size)	✓* (BL ↗ with mesh size)
	Targeted/Fished taxa	✗	✓*** (BM ↗ in sole/hake fisheries)	✓** (BL ↗ in sole/hake fisheries)	✗	∅	∅
	Acoustic deterrent?	✗	∅	✓* (BL ↗ in presence of deterrent)	✗	∅	✗

This table presents a synthesis of the results of all statistical analyses conducted to test the by-catch phenotype sensitivity (i.e. the likelihood of by-catch as a function of individuals’ traits) or vulnerability (i.e. trait-specific by-catch susceptibility to fishing techniques). To simplify the presentation of the results, we have only presented here sensitivity analyses using stranding data (much more robust than analyses using declared/observed data: see Methods) and covariates from vulnerability models with at least one significant effect on the traits of by-caught individuals. Vulnerability analyses on BM were conducted using both observation/declaration data, while analyses on sex and BL were conducted using observation data only. First sensitivity analyses, without covariates, used non-parametric comparison tests (Fisher test for sex, Wilcoxon test for BL): all methods and detailed statistics can be found in the Methods and Results sections. For all other analyses, (generalised) linear models were used: all methods and detailed statistics can be found in Methods and Appendix (Tables S2 and S6). The presence or absence of significant effects is indicated by the symbols ✓ and ✗, respectively. The symbol ∅ indicates that the test was not performed for methodological reasons (too high collinearity, not enough data to analyse, too imprecise data; see Methods and Appendix: Section S5). Below the ✓ symbol we indicated the direction of the effects (Figures 1 to 5, Tables S3, S4, S7). Next to the ✓ symbol, we indicated the level of significance of the effects (see scale below). For sensitivity analyses, when significant effects on male and female BL were similar, we only indicated the lowest significance level between the two. Abbreviations used in the table are listed below.

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

BM: Body Mass; BM: Body Length; BoB: Bay of Biscay; BM: Body Mass; ♂: Male individuals; ♀: Female individuals

Figures Captions

Figure 1: Distribution of by-caught and stranded individuals’ phenotypic traits. These figures show the distribution of BM, BL, and sex for both common dolphin and harbour porpoise incidentally captured individuals (considering only stranded individuals with marks of incidental capture, and both observation and declaration by-catch data). We displayed the distribution of continuous traits such as BL and BM using a combination of box and violin plots for each sex (except for observation and declaration data where sex information is too incomplete, as declarations did not include the sex of by-caught individuals). Meanwhile, data on the sex of by-caught individuals are displayed using bar plots. For comparison, we also plotted data from the literature on size at sexual maturity and asymptotic BL. Please refer to the legend for the original publication where these estimates came from. Other close estimates can be found in Murphy et al. (2009), but also in Ferrero and Walker (1995) and Perrin and Reilly (1984).

Figure 2: Spatio-temporal variations in stranded common dolphins’ phenotype. The figures show the expected marginal effects of the spatio-temporal variables (ICES division, trimester, year interval) on the sex (logistic regression: first two graphs) or BL (linear regression) of stranded common dolphins with external evidence of by-catch. Results were obtained using the `ggemmeans` function of the `ggeffects` `R` package (Lüdecke 2018). Dark dots indicate the predicted value of BL or sex probability as a function of spatio-temporal variables. Error bars indicate the confidence intervals based on standard errors, assuming a normal distribution. Note that we generated these graphs from models with untransformed variables, but when we used transformed variables, we obtained nearly identical graphs.

Figure 3: Spatio-temporal variations in stranded harbour porpoises' phenotype. The figures show the expected marginal effects of the spatio-temporal variables (ICES division, trimester, year intervals) on the sex (logistic regression: fisrt graph) or BL (linear regression) of stranded harbour porpoises with external evidence of by-catch. Results were obtained using the `ggemmeans` function of the `ggeffects R` (Lüdecke 2018). Dark dots indicate the predicted value of BL or sex probability as a function of spatio-temporal variables. Error bars indicate the confidence intervals based on standard errors, assuming a normal distribution. Note that we generated these graphs from models with untransformed variables, but when we used transformed variables, we obtained nearly identical graphs.

Figure 4: Effects of fishing gear and mesh size on BM and BL of by-caught harbour porpoises. The figures show the predicted marginal effects of fishing gear and mesh size on by-caught harbour porpoises' BM (Body Mass) or BL (Body Length). Results were obtained using the `ggemmeans` function of the `ggeffects R` (Lüdecke 2018). The original data points are shown in grey and slightly jittered (small amount of random variation in the location of the data points, to avoid overplotting) to improve readability. The predicted value of BM or BL is shown as dark lines or dots, as a function of mesh size or fishing gear, respectively. Grey areas and error bars indicate confidence intervals based on standard errors, assuming a normal distribution.

Figure 5: Effects of fishing gear and mesh size on BM and BL of by-caught common dolphins. The figures show the expected marginal effects of fishing gear and fished/targeted taxa on the BM or BL of by-caught common dolphins. Results were obtained using the `ggemmeans` function of the `ggeffects R` (Lüdecke 2018). The original data points are shown in grey and slightly jittered (small amount of random variation in the location of the data points, to avoid

overplotting) to improve readability. Dark dots indicate the predicted value of BM or BL as a function of fishing gear or fished/targeted taxa. Error bars indicate the confidence intervals based on standard errors, assuming a normal distribution.

Figures

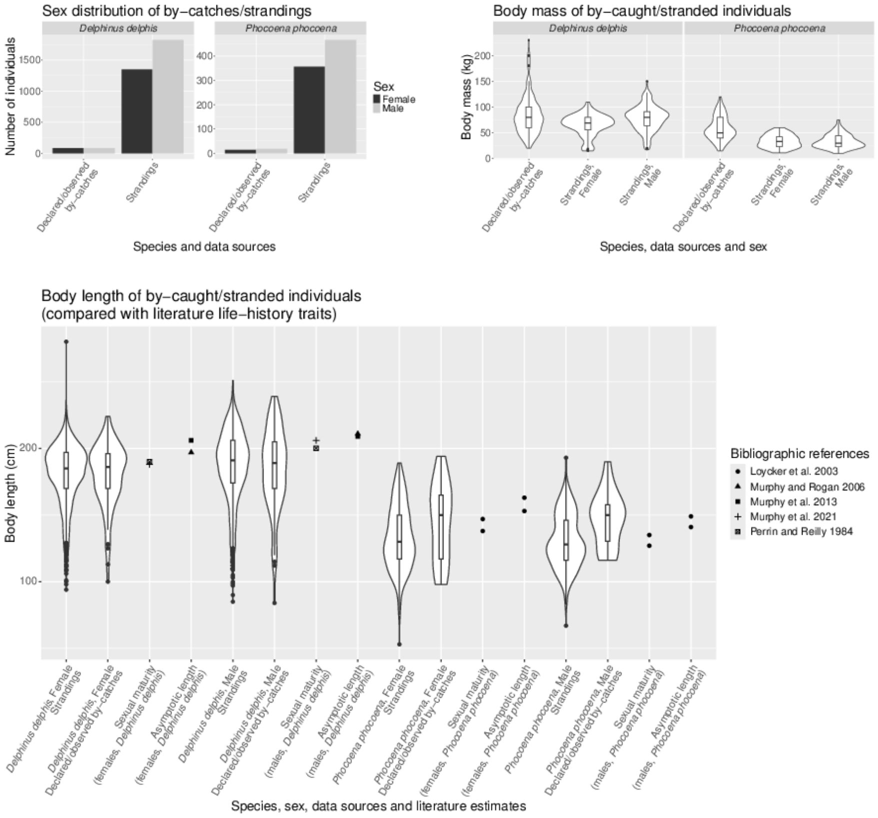
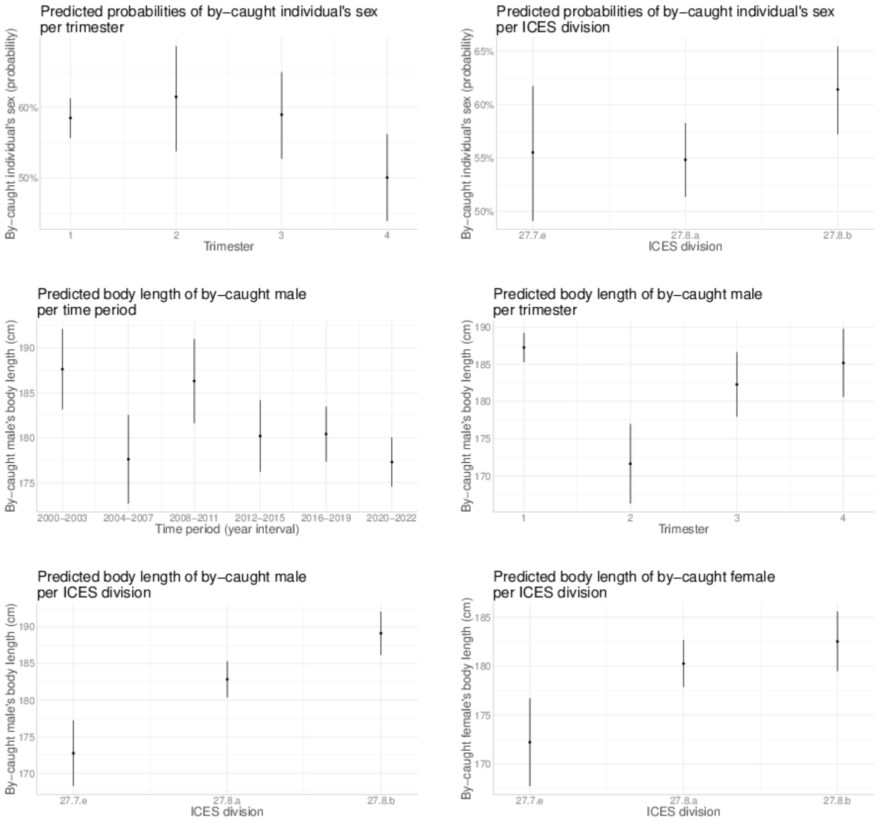


Figure 1



Predicted probabilities of by−caught individual's sex per trimester

Predicted probabilities of by−caught individual's sex per ICES division

Predicted body length of by−caught male per time period

Predicted body length of by−caught male per trimester

Predicted body length of by−caught male per ICES division

Predicted body length of by−caught female per ICES division

Figure 2

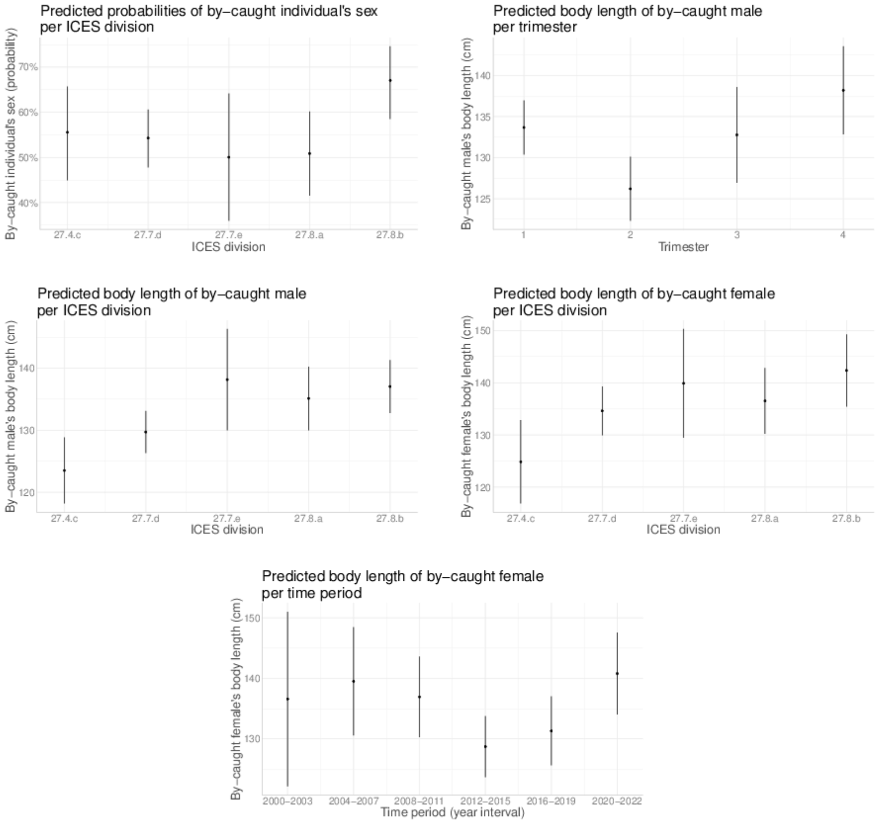


Figure 3

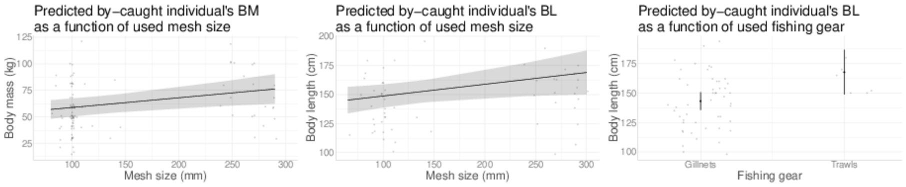


Figure 4

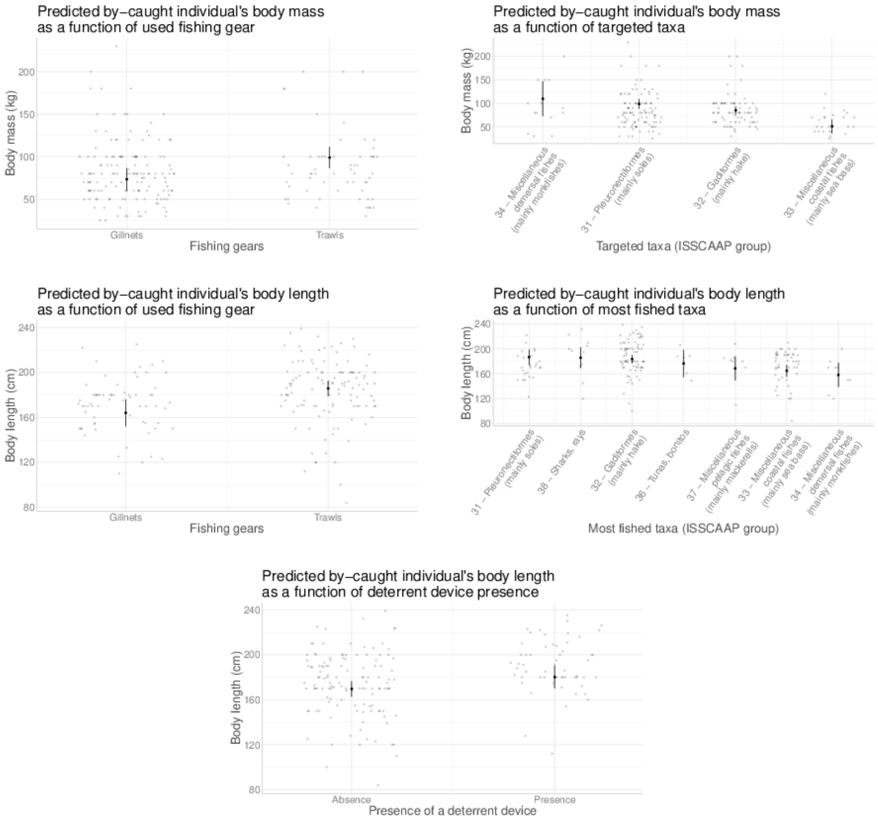

Predicted by–caught individual's body mass as a function of used fishing gear
Body mass (kg)
50
100
150
200
Gillnets
Trawls
Fishing gears
Predicted by–caught individual's body mass as a function of targeted taxa
Body mass (kg)
50
100
150
200
34 – Miscellaneous demersal fishes (mainly monkfishes)
31 – Pleuronectiformes (mainly soles)
32 – Gadiformes (mainly hake)
33 – Miscellaneous coastal fishes (mainly sea bass)
Targeted taxa (ISSCAAP group)
Predicted by–caught individual's body length as a function of used fishing gear
Body length (cm)
80
120
160
200
240
Gillnets
Trawls
Fishing gears
Predicted by–caught individual's body length as a function of most fished taxa
Body length (cm)
80
120
160
200
240
31 – Pleuronectiformes (mainly soles)
38 – Sharks, rays
32 – Gadiformes (mainly hake)
36 – Tunas, bonitos
37 – Miscellaneous pelagic fishes (mainly mackerells)
33 – Miscellaneous coastal fishes (mainly sea bass)
34 – Miscellaneous demersal fishes (mainly monkfishes)
Most fished taxa (ISSCAAP group)
Predicted by–caught individual's body length as a function of deterrent device presence
Body length (cm)
80
120
160
200
240
Absence
Presence
Presence of a deterrent device

Figure 5