



Universitat
de les Illes Balears

DOCTORAL THESIS

2021

**MONITORING COASTAL FISH THROUGH REMOTE
UNDERWATER CAMERAS: DETECTABILITY,
ABUNDANCE, VULNERABILITY AND FUTURE
APPLICATIONS**

Guillermo Follana Berná



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Doctoral Programme in Marine Ecology

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UNDERWATER CAMERAS: DETECTABILITY,
ABUNDANCE, VULNERABILITY AND FUTURE
APPLICATIONS**

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Doctor by the Universitat de les Illes Balears

List of publications included in this doctoral thesis

1. **Chapter I: Follana-Berná, G.**, Palmer, M., Campos-Candela, A., Arechavala-Lopez, P., Diaz-Gil, C., Alós, J., Catalan, I., Balle, S., Coll, J., Morey, G., Verger, F., Grau, A., 2019. Estimating the density of resident coastal fish using underwater cameras: accounting for individual detectability. *Mar. Ecol. Prog. Ser.* 615, 177–188. doi:[10.3354/meps12926](https://doi.org/10.3354/meps12926)
2. **Chapter II: Follana-Berná, G.**, Palmer, M., Lekanda-Guarrotxena, A., Grau, A., Arechavala-Lopez, P., 2020. Fish density estimation using unbaited cameras: Accounting for environmental-dependent detectability. *J. Exp. Mar. Bio. Ecol.* 527, 151376. doi:[10.1016/j.jembe.2020.151376](https://doi.org/10.1016/j.jembe.2020.151376)
3. **Chapter III: Follana-Berná, G.**, Pablo Arechavala-Lopez, P., Ramirez-Romero, E., Koleva, E., Grau, A., Palmer, M. 2021. Mesoscale assessment of sedentary coastal fish density using vertical underwater cameras. *Fish. Res.* (Under review)
4. **Chapter IV: Follana-Berná, G.**, Palmer, M., López-Aguilar, M., Grau, A., Arechavala-Lopez, P. 2021. Influence of environmental and social interactions on fish vulnerability to angling. *Fish. Res.* (Under review)
5. **Chapter V: Follana-Berná, G.**, Palmer, M., Campos-Candela, A., Alós, J., Ospina-Alvarez, A., Grau, A., Lowerre-Barbieri, S., Arechavala-Lopez, P., 2021. Consequences of trait-selective fisheries on population reproductive potential: An experimental approach. *Fish. Res.* 239, 105939. doi:[10.1016/j.fishres.2021.105939](https://doi.org/10.1016/j.fishres.2021.105939)

Information of the journals where they have been published

Chapter	Journal	Impact Factor*	Quartile	Category	Status
I	Marine Ecology Progress Series	2.824	24/110 Q1	Marine & Freshwater biology	Published
II	Journal of Experimental Marine Biology and Ecology	2.171	40/110 Q2	Marine & Freshwater biology	Published
III	Fisheries Research	3.284	20/55 Q1	Aquatic science	Under review
IV	Fisheries Research	2.422	20/55 Q2	Fisheries	Under review
V	Fisheries Research	2.422	20/55 Q2	Fisheries	Published

* last year available 2020

List of publications not included but related with this doctoral thesis

1. Díaz-Gil, C., Smee, S.L., Cotgrove, L., **Follana-Berná, G.**, Hinz, H., Marti-Puig, P., Grau, A., Palmer, M., Catalán, I.A., 2017. Using stereoscopic video cameras to evaluate seagrass meadows nursery function in the Mediterranean. *Mar. Biol.* 164, 137. doi:[10.1007/s00227-017-3169-y](https://doi.org/10.1007/s00227-017-3169-y)
2. Ospina-Alvarez, A., de Juan, S., Alós, J., Basterretxea, G., Alonso-Fernández, A., **Follana-Berná, G.**, Palmer, M., Catalán, I.A., 2020. MPA network design based on graph theory and emergent properties of larval dispersal. *Mar. Ecol. Prog. Ser.* 650, 309–326. doi:[10.3354/meps13399](https://doi.org/10.3354/meps13399)
3. Aspillaga, E., Arlinghaus, R., Martorell-Barceló, M., Follana-Berná, G., Lana, A., Campos-Candela, A., Alós, J., 2021. Performance of a novel system for high-resolution tracking of marine fish societies. *Anim. Biotelemetry* 9, 1. doi:[10.1186/s40317-020-00224-w](https://doi.org/10.1186/s40317-020-00224-w)

Acknowledgement/Agradecimientos

Me gustaría comenzar agradeciendo a mis tres directores el enorme esfuerzo y dedicación para que pueda presentar esta tesis. Miquel, Amalia y Pablo, sin vosotros y vuestra ayuda nunca podría haber llegado a este objetivo. Cada uno de vosotros me ha aportado algo diferente que ha conseguido formar a la persona que soy ahora, apoyándome moral y psicológicamente en los momentos en que esta labor se hace difícil. Gracias a vosotros he absorbido tal cantidad de conocimiento, vital y científico, que echando la vista atrás creo que si no hubiera hecho esta tesis jamás lo hubiera obtenido.

También quiero agradecer a todo el personal del Laboratorio de Andratx (LIMIA) que me ha soportado durante estos años perturbándolos con mis experimentos por todas partes. Elena, Gaetano, María del Mar, Inma, Guillem, Quique, José María, muchas gracias por todo.

Querría también agradecer a todos los compañeros del grupo Fish Ecology del IMEDEA por recibirme con los brazos abiertos y enseñarme tantísimas cosas de este mundo de la Ecología Marina. Beatriz, Ignaci, Pep, Martina, Eneko, Silvia, Elka, Amaya, Arancha, Marija, Hilmar y Ana, muchas gracias por todo.

Andrea, tú también formaste parte de este grupo, pero mereces que te mencione a parte por la ayuda indispensable que me aportaste durante los años que coincidimos, tanto en el laboratorio como en el campo, y durante los experimentos en ambos ámbitos. Rebasas energía contagiosa por todas partes y de gran ayuda en los momentos de bajón, muchas gracias.

Carlos, tú también mereces un agradecimiento especial. Aunque acabaste la tesis un año después de mi incorporación eso no hizo que no tuviéramos una muy buena amistad. Te agradezco muchísimo el recibimiento que me diste, fuiste lo más parecido a un anfitrión explicándome cosas de ambos centros de investigación donde trabajamos (LIMIA e IMEDEA) e introduciéndome en la vida social de la isla. Junto con tu mujer Merit, a la que también le agradezco muchísimo, me hicisteis sentir como en una familia lejos de la mía. Carlota y Roc, también formasteis parte de esa familia, fuisteis los principales culpables de que saliera de fiesta por la isla, esos días de desconexión eran geniales, por lo que también estaré eternamente agradecido.

Edu, te considero un amigo excepcional, al que siempre pude recurrir en los momentos que necesitaba ayuda para realizar los muestreos de campo. Después sabía que podría disfrutar de un buen baño en alguna cala idílica de la isla, al final de casi morir de insolación. Muchas gracias por las risas.

También agradecerles a todos mis compañeros de IMEDEA con los que tanto tiempo he pasado, tanto en el ágora a la hora de comer, como después del trabajo tomando alguna cerveza o directamente de fiesta. Xisca, Javi, Chema, Jaime, Eugenio, Vicenç, David, Miguel, Alex, Albert, Eva, mi compi de despacho Lucia, Marina, Paula, Susana, Vero, Almu, Melo... supongo que me dejo alguno, pero quien lea estos agradecimientos y sienta que haya formado parte de esta gran familia IMEDEICA, que sepan que también se pueden sentir aludidos.

A todos los estudiantes de Grado y Master que estuvieron en el grupo ayudándome. Mario tú fuiste uno de ellos y mírate ahora, también haciendo un doctorado; no sabes dónde te has metido... Muchas gracias por tu ayuda y amistad.

Agradecerle a Guillem, mi compañero de piso durante tantos años, el tiempo pasado juntos, cocinando, saliendo a tomar el aire, las charlas en la cocina hablando de ciencia y otras “cosas”. Has sido un gran apoyo durante todos esos años.

Agradecerles a mis tíos mallorquines, Ángeles y Carlos junto con mis primos Laura y Carlos que me recibieron en la isla con los brazos abiertos. A mi hermano Jorge, quien nos ha entusiasmado con una nueva generación, Valentina.

Pero a los que de verdad hay que agradecerles que esta tesis pueda existir es a mis padres. La dedicación que han mostrado en criar a dos hijos y el esfuerzo que han puesto en ello es admirable, espero devolvérselo multiplicado en algún momento de mi vida. Espero que os sintáis orgullosos de lo que habéis creado.

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Lists of Acronyms, Figures and Tables

List of Acronyms

ANCOVA Analysis of covariance.

BCI Bayesian credibility interval.

BRUV Baited remote underwater video.

CPUE Captures per unit effort.

DIC Deviance Information Criterion.

GMT Greenwich Mean Time.

GSI The gonadosomatic index.

h The maximum number of eggs produced in a day at the optimal temperature.

HR Home Range.

HV High Vulnerability.

IQR Interquartile range.

LB Latency to bite the bait.

LV Low Vulnerability.

MCMC Monte Carlo Markov chains.

MPA Marine Protect Area

MV Medium Vulnerability.

PID Probability of individual detection.

POLS Pace-of-life syndrome.

Rhat Potential scale reduction factor.

RUV Remote underwater video.

SD Standard deviation.

SRMSE Scaled root mean squared error.

Temp.optimal The estimated optimal temperature for a given tank.

tol The temperature tolerance of a given tank.

UVC Underwater visual census.

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Resumen en castellano

La gestión de la pesca recreativa es un reto particularmente difícil debido a (1) su creciente relevancia, sobre todo a lo largo de la costa mediterránea, y (2) a la escasez de datos disponibles. La relevancia de la pesca recreativa es hoy indiscutible, pero las capturas, la mortalidad por pesca, el esfuerzo pesquero, la abundancia y casi todos los descriptores de esta actividad son desconocidos o poco conocidos en la mayoría de los casos. Dificultando el conocer la dinámica de la población de las especies objetivo. Esta circunstancia impide el diseño, la implementación y la evaluación de cualquier plan de gestión con una base científica.

Por lo tanto, es urgente desarrollar métodos de observación que proporcionen datos objetivos, precisos y exactos sobre la pesca recreativa. Esta tesis tiene como objetivo llenar este vacío, explorando las capacidades de las cámaras submarinas para la obtención de estos datos.

Los avances tecnológicos experimentados por las cámaras submarinas han sido impresionantes en los últimos años. Actualmente, la calidad de la imagen, la duración de la batería, la durabilidad, la capacidad de memoria o el coste de éstas ya no son factores limitantes para su uso. Sin embargo, las imágenes subacuáticas deben traducirse en datos cuantitativos, necesarios para diseñar planes de gestión adecuados y que estén de acuerdo con los procesos ecológicos subyacentes. La conexión de imágenes y datos está lejos de ser banal.

En concreto, he explorado cómo obtener datos para dos variables particularmente difíciles: la abundancia de peces y la vulnerabilidad de los peces a la pesca con caña. En

el caso de la abundancia de peces, el primer paso fue combinar cámaras sin cebo y con visionado de campo horizontal con uno de los métodos más populares utilizados para estimar la abundancia de peces costeros: buceadores que cuentan peces a lo largo de transectos (es decir, censos visuales submarinos o UVC). He demostrado cómo combinar cámaras con UVCs para explorar y tener en cuenta cualquier dependencia ambiental o de las características de los peces en la detectabilidad de éstos y, lo que es más importante, he demostrado que una vez estimada la detectabilidad de los peces, la abundancia de éstos puede ser estimada con precisión y exactitud sólo mediante cámaras. Este hecho tan destacable abre la posibilidad de estimar la abundancia de peces a escalas espaciales y temporales relevantes para gestionar la pesca recreativa, siempre que el número de cámaras y el tiempo de implantación de éstas no sean factores limitantes.

El siguiente paso fue resolver dos problemas pendientes: (1) el área mostrada por las cámaras sin cebo con visionado de campo horizontal no se puede estimar con precisión y (2) el método estadístico desarrollado para las cámaras proporciona valores de abundancia a la escala del método de referencia, en este caso, los UVC. A pesar de ser el estándar más común, también se reconoce que los UVC pueden introducir algunos sesgos a la hora de estimar la abundancia de peces. En consecuencia, se desarrolló un nuevo diseño de cámaras sin cebo con visionado de campo vertical, un nuevo protocolo de muestreo y un nuevo análisis estadístico. He demostrado que este nuevo marco produce estimaciones de la abundancia de peces de manera más precisa y exacta. Posteriormente, el tercer paso fue demostrar la aplicabilidad y la viabilidad de determinar la abundancia de peces a gran escala, tanto espacial como temporal. Como prueba de concepto, se estimó con éxito la abundancia de una especie de serránido objetivo de la pesca recreativa (*Serranus scriba*), a lo largo de más de 100 km de la costa sur de Mallorca. Además, este

diseño permitió identificar los principales factores ecológicos que se correlacionan con la abundancia de peces. Por ejemplo, demostré que la abundancia de peces se correlaciona negativamente con la exposición a la pesca.

En cuanto a la vulnerabilidad de los peces, he utilizado cámaras cebadas para averiguar los patrones de correlación de una variable sustituta (el tiempo de latencia hasta que el pescado muerde el cebo) con diversas variables relacionadas con los complejos procesos subyacentes. Los resultados evidenciaron que las interacciones pez-pez (sociales) juegan un papel relevante en la probabilidad de que un pez específico sea capturado. Los resultados reportados aquí sugieren firmemente que se debería encontrar una explicación mecanicista de los procesos que configuran la vulnerabilidad de los peces con el fin de mejorar el diseño de planes de gestión. En caso contrario, la pesca recreativa puede llegar a generar poblaciones con un gran porcentaje de peces no vulnerables, lo que no sólo es indeseable ecológicamente, sino que también afecta a la satisfacción de los pescadores.

Finalmente, hemos explorado en profundidad una de las consecuencias ecológicas de la vulnerabilidad. Los marcos teóricos existentes plantean la hipótesis de que los peces no vulnerables pueden tener un potencial reproductivo menor que el de los peces vulnerables. En consecuencia, he desarrollado un método para cuantificar la vulnerabilidad de los peces y lo he aplicado para diseñar grupos experimentales en cautividad, emulando poblaciones con una vulnerabilidad media diferente. Los resultados demuestran que ni el número de huevos puestos ni el patrón de puesta estacional están relacionados con la vulnerabilidad de los peces. Por el contrario, la calidad de los huevos producidos por los peces no vulnerables parece ser mayor al final de la temporada de

puesta que la de los peces vulnerables. Si la calidad de los huevos afecta la capacidad de supervivencia y dispersión de estos, los resultados de este hallazgo se deben explorar y tener en cuenta a la hora de diseñar planes de gestión espacial.

Para terminar, esta tesis ha alcanzado su objetivo principal: desarrollar técnicas de muestreo viables y fiables basadas en cámaras subacuáticas, que produzcan datos precisos y exactos ya listos para ser utilizados para la evaluación de la pesca recreativa y de otras pesquerías con carencia de datos.

Resum en català

La gestió de la pesca recreativa és un repte particularment difícil a causa de (1) la seva creixent rellevància, sobretot al llarg de la costa mediterrània, i (2) de l'escassetat de dades disponibles. La rellevància de la pesca recreativa és avui indiscutible, però les captures, la mortalitat per pesca, l'esforç pesquer, l'abundància i gairebé tots els descriptors d'aquesta activitat són desconeguts o poc coneguts en la majoria dels casos. Per tant, també es desconeix la dinàmica de la població de les espècies objectiu. Aquest fet impedeix el disseny, la implementació i l'avaluació de qualsevol pla de gestió amb una base científica.

Per tant, és urgent desenvolupar mètodes d'observació que proporcionin dades objectives, precises i exactes sobre la pesca recreativa. Aquesta tesi té com a objectiu omplir aquest buit explorant-ne les capacitats de les càmeres submarines.

Els avenços tecnològics experimentats per les càmeres submarines han estat impressionants en els darrers anys. Actualment, la qualitat de la imatge, la durada de la bateria, la durabilitat, la capacitat de memòria o el cost d'aquestes ja no són factors limitants. Tot i això, les imatges subaquàtiques s'han de traduir en dades quantitatives, necessàries per dissenyar plans de gestió adequats, d'acord amb els processos ecològics subjacents. La connexió entre imatges i dades és lluny de ser banal.

En concret, vaig explorar com generar dades per a dues variables particularment difícils: l'abundància de peixos i la vulnerabilitat dels peixos a la pesca amb canya. En el cas de l'abundància de peixos, el primer pas va ser combinar càmeres sense esca amb visionat de camp horitzontal amb un dels mètodes més populars que s'utilitzen actualment

per estimar l'abundància de molts de peixos costaners: bussejadors que compten peixos al llarg de transectes (és a dir, censos visuals submarins o UVC). Vaig demostrar com combinar càmeres i UVC per explorar i tenir en compte qualsevol dependència ambiental o del les característiques dels peixos amb la detectabilitat d'aquests i, el que és més important, vaig demostrar que un cop estimada la detectabilitat dels peixos, l'abundància d'aquests pot ser estimada amb precisió i exactitud només mitjançant càmeres. Aquest fet tan destacable obre la possibilitat d'estimar l'abundància de peixos a escales espaials i temporals rellevants per gestionar la pesca recreativa, sempre que el nombre de càmeres i el temps de desplegament d'aquestes no siguin factors limitants.

El següent pas va ser resoldre dos problemes pendents: (1) l'àrea que mostren les càmeres sense esca amb visionat de camp horitzontal no es pot estimar amb precisió i (2) el mètode estadístic desenvolupat per a les càmeres proporciona valors d'abundància a l'escala del mètode de referència, que en aquest cas són els UVC. Tot i ser un dels 'estàndards més comuns, també es reconeix que els UVC poden introduir alguns biaixos a l'hora d'estimar l'abundància de peixos. En conseqüència, es va desenvolupar un nou disseny de càmeres sense esca amb visionat de camp vertical, un nou protocol de mostreig i una nova anàlisi estadística. Vaig demostrar que aquest nou marc produeix estimacions de l'abundància de peixos de manera més precisa i exacta. Després, el tercer pas va ser demostrar l'aplicabilitat i la viabilitat de controlar l'abundància de peixos a gran escala, tant espaiial com temporal. Com a prova de concepte, es va estimar amb èxit l'abundància d'un serranid que és una espècie objectiu de la pesca recreativa (*Serranus scriba*), al llarg de més de 100 km de la costa sud de Mallorca. A més, aquest disseny va permetre identificar els principals factors ecològics que es correlacionen amb l'abundància de

peixos. Per exemple, vaig demostrar que l'abundància de peixos es correlaciona negativament amb l'exposició a la pesca.

Pel que fa a la vulnerabilitat dels peixos, he utilitzat càmeres amb esca per esbrinar els patrons de correlació d'una variable substituïda (el temps de latència fins que el peix ataca l'esca) amb diverses variables relacionades amb els complexos processos subjacents. Els resultats van evidenciar que les interaccions peix-peix (socials) juguen un paper rellevant en la probabilitat que un peix específic sigui capturat. Els resultats reportats aquí suggereixen fermament que s'hauria de trobar una explicació mecanicista als processos que configuren la vulnerabilitat dels peixos per tal de millorar el disseny de plans de gestió. En cas contrari, la pesca recreativa pot arribar a generar poblacions amb un gran percentatge de peixos no vulnerables, cosa que no només és indesitjable ecològicament, sinó que també afecta la satisfacció dels pescadors.

Finalment, he explorat en profunditat un dels conseqüències ecològiques de la vulnerabilitat. Els marcs teòrics existents plantegen la hipòtesi que els peixos no vulnerables poden tenir un potencial reproductiu menor que els peixos vulnerables. En conseqüència, he desenvolupat un mètode per quantificar la vulnerabilitat dels peixos i l'he aplicat per dissenyar grups experimentals en captivitat, emulant poblacions amb una vulnerabilitat mitjana diferent. Els resultats demostren que ni el nombre d'ous posats ni el patró de posta estacional estan relacionats amb la vulnerabilitat dels peixos. Per contra, la qualitat dels ous produïts pels peixos no vulnerables sembla ser més gran al final de la temporada de posta que la dels peixos vulnerables. Si la qualitat dels ous afecta la capacitat de supervivència i dispersió d'aquests, els resultats d'aquesta troballa s'han d'explorar i tenir en compte a l'hora de dissenyar plans de gestió espacial.

Per acabar, aquesta tesi ha assolit el seu objectiu principal: desenvolupar tècniques de mostreig viables i fiables basades en càmeres subaquàtiques, per a produir dades precises i exactes ja llestes per ser utilitzades per l'avaluació de la pesca recreativa i d'altres pesqueries amb manca de dades.

Abstract

Managing recreational fishing is particularly challenging because of (1) its growing relevance, particularly along the Mediterranean coast, and (2) the scarcity of data available. The relevance of recreational fishing is nowadays indisputable, but catches, fishing mortality, fishing effort, abundance and almost all the descriptors of this activity are unknown or poorly known in most of the cases. Thus, population dynamics of the target species remains unknown too. This fact precludes the design, implementation, and evaluation of any scientifically based management plan.

Therefore, there is an urgent need for developing observation methods that supply objective, precise, and accurate data on recreational fishing. This thesis is aimed to fulfill this gap by exploring the capabilities of underwater cameras.

The technological advances experienced by underwater cameras has been impressive in the recent years. Nowadays, image quality, battery life, durability, memory capability or cost are no longer limiting factors. However, the underwater images must be distilled into the quantitative data needed for designing proper management plans in accordance with the underlying ecological processes. Connecting images and data is far to be trivial.

Specifically, I explored how to deliver data for two particularly challenging variables: fish abundance and fish vulnerability to angling. In the case of fish abundance, the first step was to combine unbaited cameras with horizontal field view with one of the most popular methods currently used for estimating abundance of many costal fish: scuba divers counting fish along transects (i.e., underwater visual censuses, or UVCs). I

demonstrated how to combine cameras and UVCs for exploring and accounting for any environmental or fish dependencies on fish detectability and, more important, I proved that once fish detectability has been estimated, fish abundance could be precisely and accurately estimated using only cameras. Provided that the number of cameras and the deployment time are not limiting factors, this fact opens the possibility of estimating fish abundance at spatial and temporal scales relevant for managing recreational fisheries.

The second step was to solve two pending problems: (1) the area surveyed by unbaited cameras with horizontal view cannot be precisely estimated and (2) the statistical method developed for the cameras renders abundance values at the scale of the reference method, which is, in this case, UVC. In spite of being the common standard, it is also recognized that UVC may introduce some biases when estimating fish abundance. Accordingly, a new design of unbaited cameras with vertical view, a new sampling protocol, and a new statistical analysis were developed. I demonstrated that this new framework produces estimates of fish abundance more precise and more accurate. The third step was to demonstrate the applicability and feasibility of monitoring fish abundance at large spatial and temporal scale. As a proof-of-concept, the abundance of a small serranid targeted by recreational fishers (*Serranus scriba*) was successfully estimated along more than 100 km of the South coast of Mallorca. Moreover, this design allowed identifying the main ecological drivers that are correlated with fish abundance. For example, I demonstrated that fish abundance is negatively correlated with exposure to fishing.

Concerning fish vulnerability, I used baited cameras for disentangling the correlational patterns of a surrogate variable (latency time until a fish attacks the bait)

with several variables related with the complex underlying processes. The results evidenced that fish-fish (social) interactions play a relevant role in the odds a specific fish has of being captured. The results reported strongly suggest that a mechanistic understanding of the processes shaping fish vulnerability should be unravelled in order to improve the design of appropriate management plans. Otherwise, recreational fishing may lead to populations with a large percentage of non-vulnerable fish, which is not only ecologically undesirable but also affects fisher's satisfaction.

Finally, I have in-depth explored one of the ecological outcomes of vulnerability. The existing theoretical frameworks hypothesize that non-vulnerable fish may depict smaller reproductive potential than vulnerable fish. Accordingly, I have developed a method for scoring fish vulnerability, and I have applied it to design experimental groups in captivity, emulating populations with a different average vulnerability. The results demonstrate that neither the number of eggs laid, nor the seasonal spawning pattern is related with fish vulnerability. Contrasting, the quality of the eggs quality of non-vulnerable fish seems to be higher toward the end of the spawning season than that of vulnerable fish. Provided that egg quality is affecting survival and dispersal capability, the outcomes of this finding should be explored and accounted for when designing spatial management plans.

Overall, this thesis has achieved its primary objective: to develop feasible and reliable sampling frameworks based on underwater cameras that produce accurate and precise data ready to be used for assessing recreational fishing and other poor-data fisheries.

General Introduction

Fish Populations and Fishing Management

One of the main challenges that researchers and managers are facing, both in terrestrial and aquatic environments, is trying to know as accurately and precisely as possible the number of individuals in a population. Estimating abundance is always complex, but the characteristics of aquatic environments imposes additional challenges. Marine environments cover over 71% of the surface of the Earth and are structurally less accessible than the terrestrial ones, which that they remain poorly known, despite the growing effort invested.

Accordingly, one of the fundamental challenges in marine ecology and fisheries science is to describe the current state of fish populations in terms of abundance, which is imperative for understanding population dynamics, (Agnew et al., 2013; Hilborn and Walters, 1992). However, reliable abundance data at relevant spatio-temporal scales are rarely available in marine systems. Data scarcity is especially severe in the cases of recreational and artisanal fisheries targeting coastal fish, for which science-based sustainable management is often unfeasible (Pita et al., 2018). In addition, even in well-monitored fisheries, most of the data come from catches and the biases of this data source are widely recognized (Kleiber and Maunder, 2008). Consequently, it is advisable to provide accurate, scientifically validated information to support the decisions making when managing fish populations and fisheries resources.

Although the strength and extend of overfishing is still under debate (Pauly et al., 2013), commercial fishing has traditionally been identified as the main source of fish

catches but there is growing concern about the potential impact of recreational fishing on fishery resources (Cooke and Cowx, 2006; Lewin et al., 2006). It is estimated that the annual catches of recreational anglers worldwide can reach 47 billion fish per year, which represents more than half of the global catches of commercial fishing, although approximately two thirds of the recreational catches are released (Cooke and Cowx, 2006). The socioecological and economical importance of the recreational fisheries is nowadays being increasingly recognized (Arlinghaus et al., 2019), and in many places, such as the Mediterranean, it is common that this practice displays an increasing trend, which contrasts with the declining trend of traditional fisheries (Grau, 2008). In regards of the Balearic Islands, many people carry out this activity typically close to the coast. The numbers of participants do not stop to increase, but the information available on catches and effort is still poorly known (Gordoa et al., 2019; Morales-Nin et al., 2015). Currently, the coastal areas worldwide suffer a high anthropogenic pressure and experience the immediate effects of climate change (Savo et al., 2017). Aimed to face all these threats, decision-making tools for better fish conservation and fisheries management in coastal areas are constantly advancing (Long et al., 2015). Nevertheless, reliable methods to obtain the data needed for evaluating the monitoring programs are essential for improving decision-making strategies. In this line, the *Marine Strategy Framework Directive* is aimed to provide a scientifically founded advice to management programs. The ecosystem approach to fisheries and the marine spatial planning are examples of the framework resulting from such a science-management cooperation. However, these worthy intentions may lead nowhere if not supported by the development and on-site application of effective methods to survey fish stocks and quantify fish population dynamics in a reliable and accurate way, which must be adapted to the case-

specific conditions to successfully meet the complex and critical challenges of conserving and managing fishery resources.

Monitoring tools for assessing marine fish populations

With the rise of the modern natural sciences, diverse tools and methods have been developed to explore marine environments, from the littoral zone to open waters, from the shelf to the abyssal seafloor (Murphy and Jenkins, 2010). Scientists extract data using diverse methods: From those emulating fishing to the most recent technological innovations as, for example, the use of autonomous, remotely controlled vehicles. Technological advances have decisively contributed to successful marine field studies at many levels: from individuals to populations, to meta-populations, to communities, and to entire ecosystems (Devine and Jensen, 2018). Different methods have been developed and applied to assess fish populations under management. Conventional fishing gears has been used either, directly exploiting the data provided by the fishers or reported by on-board observers, or included within scientifically rigorous survey designs. These methods are not only invasive for the environment but also potentially biased. Traps, hooks or nets are known to experience some behaviour or size selectivity (i.e., the catches are not a random sample of the fish). Moreover, most of them are time and effort consuming. Contrasting, fishing-dependent methods can cover broad spatial areas and wide environmental ranges (Murphy and Jenkins, 2010). Therefore, fishing-dependent methods not only can cause some environment damage, such as the specific case of trawling surveys (Spedicato et al., 2019; Trenkel et al., 2019), but also provide potentially biased data.

On the other hand, other non-invasive, fishing independent methods has been developed to monitor coastal fish populations. Among them, one of the most widely used method is the direct observations by divers that follow some standardized protocol, known as underwater visual censuses (UVCs) (Murphy and Jenkins, 2010). UVCs has been extensively used to quantify spatial distribution, species richness, abundance and size distribution of fishes in shallow marine habitats (Edgar et al., 2004). UVCs can be based in either transects or fixed points. Depending on water depth and environmental conditions, snorkelling and scuba diving have been used. It has been claimed that UVCs provide accurate and precise data on conspicuous, sedentary fish species, but surveys can be biased, among many other factors, by the observer experience and by the diver presence itself. Advantages and disadvantages of UVCs for estimating fish abundance and diversity have been reported and discussed in several papers (Dickens et al., 2011; Kulbicki et al., 2010; Thompson and Mapstone, 1997; Trevor et al., 2000). For example, UVCs has been claimed to allow replication (which may increase the statistical power for testing the hypothesis under evaluation), to afford surveys at large areas, to estimate fish sizes, or to describe species-specific habitat preferences. Some additional advantages have been proposed: UVCs are environment-friendly and the data recorded by the divers can be readily exploited. On the contrary, some disadvantages of UVCs can be signalled: the observers must be thoroughly trained, observations are prone to some subjective interpretation, water visibility must reach a minimum threshold, and scuba diving imposes severe security restrictions, both for depth and time. UVC observations may be biased in relation the estimated size of the fish or with the number of fish counted. These potential biases depend, among others, on the observer's experience, the spatio-temporal

variability of fish abundance and on the effects of the presence of divers on fish behaviour.

Due to these potential drawbacks and surfing on the astonishing technological advances available today, the use of underwater cameras for monitoring fish populations are currently increasing. Underwater video methods are also non-invasive and non-extractive. Moreover, underwater cameras overcame most of the limitations of UVCs related with diving security restrictions, reduce the diver/device influence on fish behaviour and allow long-term monitoring of fish populations (Cappo et al., 2003).

The two main types of camera devices are baited or unbaited. Baited remote underwater video surveys (BRUVs) are one the most widely used methods worldwide (Whitmarsh et al., 2017). However, the fact that many fish are attracted by the bait is at the same time its major potential drawback because depending on the fish-specific attractiveness, fish density can be overestimated in a unknown, species-specific way (Mallet and Pelletier, 2014). Although BRUVs allow obtaining many replicated observations, can cover many study sites and can attract a wide range of fish species, it also has a restricted field of view and, most importantly, it takes long time and effort to extract the variables of interests (i.e., fish counts) from the videos.

Remote unbaited cameras (RUVs) have been used to a lesser stand than BRUVs to monitor fish. It is also a non-invasive and non-extractive method, and presents fewer drawbacks compared to all the aforementioned methodologies (Mallet and Pelletier, 2014). It has been claimed that the application of RUVs, along with the technological opportunities offered by camera-based wildlife assessment, can revolutionize the way we monitor fish and other aquatic organisms. One of the major promises of RUVs is that fish

density (number of animals per unit area) can be properly (i.e., with accuracy and precision) from the fish counts across a relatively few video frames (Campos-Candela et al., 2018). However, RUVs also have certain objections to be solved or assumptions to be checked before this methodology can be routinely applied as a monitoring tool for coastal fisheries resources. One of the key assumptions for extracting absolute density from RUVs is that the animal density must remain constant at the spatial and temporal scale of a given sampling event. Fortunately, this assumption is probably met by many resident coastal fish because they tend to remain within a given area of activity, called home range (HR), which are orders of magnitude smaller than the extent of suitable habitat (Alós et al., 2016; March et al., 2010; Villegas-Rios et al., 2014). For fish displaying a HR pattern of spatial occupation, no emigration, no immigration, no changes in the HR location and distribution, no birth and no death can be safely assumed at the spatial and temporal scales commonly used for sampling abundance. Another assumption is that any fish in the field view of the camera must be detected or, more precisely, detectability (i.e., the probability that a fish actually within the field of view would be detected) must be known. Therefore, the species-specific environmental dependencies of detectability should be assessed, which may be challenging. Habitat features such as the bottom roughness or seagrass cover determine the shelter landscape for a given species, thus they are expected to affect detectability (Hutto, 2016; Marques et al., 2017). Water turbidity is expected to affect detectability too. Thus, extreme cases (e.g., cryptic species that remain sheltered most of the time, or sites with limited water transparency) are inappropriate for being assessed using unbaited cameras. Fortunately, water transparency is excellent in the Balearic Islands, where many benthic species spend most of the time

swimming over the seagrass canopy or other sea bottom types, thus they are easily detectable by an underwater camera.

Detectability and Abundance of Coastal Fish using RUVs

The concept of detectability deserves special attention. Detectability, or detection probability, refers to the near-universal situation in animal population monitoring in which survey methods do not detect the presence of all animals actually present in the sampling area. Monitoring programs must, thus, incorporate methods for estimating and account for the effects of detectability, in such a way that the true, absolute fish abundance must be derived from the observed variable (e.g., fish counts) (Pollock et al., 2002). In the present thesis, the methodological protocol for the use of RUVs is progressively improved in Chapter I and Chapter II in order to develop an efficient and reliable tool for estimating absolute densities. I have selected *Serranus scriba* as model fish because is one of the most common targets of recreational fishing in the Balearic Islands (Dedeu et al., 2019). First, I demonstrate how to design a proper sampling program, in terms of number of cameras and deployment time, for achieving a predefined precision when estimating fish density. This goal was reached by means of simulations: a number of fish were moved according the movement model proposed by Campos-Candela et al., (2018). Once moving from simulations to the fieldwork, the main constraint in my case has been the recording time, since the underwater cameras depend on batteries with a limited life (3 hours). This recording time fits well with one of the method's assumptions (abundance must be constant within a sampling event), thus the number of cameras was increased

until it is guaranteed to reach the predefined precision. The simulation experiments showed that 10 cameras were enough in my case, but the simulation software produced can find the optimal combination in other cases. Other aspects to take into account has been how to properly manage the large number of videos produced, to provide storage space and, mainly, to manually extract the information from the videos. In the near future, the application of deep learning algorithms is expected to overcome the huge effort needed for extracting data from the videos (Campos-Candela et al., 2019).

At Chapter I, RUVs with horizontal field view was used and combined with conventional UVCs transects in order to better understand the environmental dependencies *S. scriba*. Fish can hide behind rocks, within the seagrass meadows and they could be hard to detect or identify at long distance when surveyed with RUVs. In addition, the area actually surveyed by horizontal RUVs cannot be precisely delimited, and this uncertainty negatively propagates on the precision of fish density. These problems were solved after designing a new camera device, with vertical field view, which is introduced in Chapter II. The area surveyed can be precisely measured for vertical RUVs. Moreover, I demonstrated that fish could be safely classified when viewed from the top.

The next step in Chapter II was to assess the environmental dependencies of detectability when using vertical RUVs. Provided that conventional UVCs are not the ground true, I designed an ad-hoc diving method for estimating the actual number of *S. scriba* in a relatively small area. This number was compared with the number of *S. scriba* counted from a video of the same area, thus allowing estimating detectability. After replicating the simultaneous (ad-hoc diving method and cameras) sampling of many sites

along all the environmental gradient of *S. scriba*, the environmental dependencies of detectability were assessed. Therefore, Chapter II demonstrates the full methodological protocol for estimating absolute fish density of *S. scriba* at any site, using vertical cameras. The feasibility of applying this method at a spatio-temporal scale relevant for adopting management decisions was demonstrated at Chapter III, where the abundance of *S. scriba* was estimated along the Southern coast of Mallorca (nearly 100 km) and at two seasons (Spring and Summer). The sampling was specifically designed for testing the correlational patterns between the abundance of *S. scriba* and recreational fishing. Furthermore, this species presents different behavioural traits regarding vulnerability to angling (Alós et al., 2015), which may have consequences on its survival, reproductive success, habitat use and distribution. All these aspects were explored at Chapter IV and Chapter V.

Vulnerability to fishing and its biological consequences

In the case of hook-and-line fishing, vulnerability is the chance that a given fish attacks the bait. Vulnerability is the result of many interrelated processes; among them, fish behaviour has a key role. Encountering a bait is not sufficient to cause a fish to strike (Monk and Arlinghaus, 2017), and lure-striking decisions by fish result from the combination of a number of factors that include encountering the angling gear, the fish interaction with the angling gear, and certain internal characteristics of the fish, including several behavioural traits and other traits correlated with behaviour, such as metabolic rate (Lennox et al., 2017). Bolder, more exploratory behavioural phenotypes can be more vulnerable to capture by angling than shyer behavioural phenotypes (Monk et al., 2021).

The relationship between boldness and vulnerability has been repeatedly tested. However, vulnerability not only depends on fish behaviour but also on many abiotic and biotic environmental factors (Lennox et al., 2017). At this regard, the social learning is a widespread mechanism in many fish species for acquiring information (Lovén Wallerius et al., 2020; Takahashi and Masuda, 2021). In this thesis, the relative importance of the social context (fish-fish interactions) on vulnerability were experimentally examined using BRUVs in Chapter IV. It is noteworthy that the experiments were completed in the natural environment. The use of BRUVs specifically designed for this assessing vulnerability has allowed exploring the correlational patterns of vulnerability in relation with several potential explanatory variables. I have made special emphasis in exploring the role of social interactions in shaping the vulnerability of *S. scriba*.

Finally, it is relevant to understand the potential consequences of vulnerability to angling on fish population dynamics. In addition to the obvious consequences of removing part of the population, I was interested in testing the existence of any effect of angling in the *per capita* reproductive potential because these effects may compromise the long-term sustainability of a population (Ospina-Alvarez et al., 2020). It seems that angling preferentially selects and removes the bolder phenotypes. Assuming that behaviour (and particularly, the behavioural traits related with vulnerability) may be at least partially heritable (Philipp et al., 2009), the long-term outcome would be that shyer phenotypes would become progressively more abundant. It seems that the repeated removal (by angling) of fish with specific, heritable behavioural traits (i.e., bolder or more active individuals (Biro and Post, 2008) may induce behavioural changes at the population level (Alós et al., 2016; Cooke et al., 2007). Angling, therefore, has the potential to render fish populations less catchable overall (Philipp et al., 2009) due to the

emergence of timidity-syndromes (Arlinghaus et al., 2017), making mechanisms of vulnerability an important concept for managers to consider when conserving, protecting, and enhancing recreational fish stocks. The vulnerability of fish to fishing depends on a range of life-history (e.g. growth, reproduction), behavioural (e.g. boldness) and physiological (e.g. metabolic rates) traits which are usually correlated with reproductive success. Based on the above, one of the hypotheses that can be raised is that more vulnerable to fishing could also be bolder, and that bolder fish, in turn, could display accelerated metabolic rate, which could be traduced in accelerated growth rate and in larger reproductive potential. The hypothesis that vulnerable fish may have greater reproductive potential was empirically evaluated in Chapter V.

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Objectives and structure

Chapter I

The use of underwater cameras without bait to obtain fish densities is being a great advance when it comes to being able to use them in a great spatial and temporal range.

Objectives: To be able to use the cameras with a precision and accuracy to other sampling methods. In this case, we focus on UVCs, but the final objective is to be able to calibrate them to be used by any method.

Hypothesis: Underwater cameras can suffer when it comes to individually detecting all the fish in an area because there may be obstacles in front of it that prevent an ideal view.

Chapter II

Horizontal cameras have been observed to present difficulties when it comes to being able to extract the number of individuals from an area because there may be obstacles in front of it that hinder their vision. Among these obstacles, the roughness of the habitat or the presence of *Posidonia oceanica* meadows may be affecting it.

Objectives: Use a structure specifically conceived to overcome obstacles that prevent horizontal cameras from observing the number of fish well. A new vertical structure is used that observes the bottom and that can work better in the different habitats of coastal species in addition the area surveyed is known.

Hypothesis: The vertical cameras, when observing from above, can see between the rocks or inside the *Posidonia oceanica*, notably improving the number of individuals capable of being seen. Habitat effects will affect it less than horizontal cameras.

Chapter III

The use of cameras can be a very powerful tool when it comes to finding absolute densities of fish in the coastal environment. Thanks to them, management programs can be improved thanks to the fact that they can sample large areas and a wide range of temporalities. In addition, the camera could be a tool that would improve methodologies dependent on fishing.

Objectives: Use vertical cameras to find the density of a shore fish, which is a target species for recreational fishing. To do this, it is intended to sample the entire south-west coast of Mallorca, more than 100 km of coastline, and see the population dynamics in a context of exposure to recreational fishing.

Hypothesis: Our target fish, the *Serranus scriba* presents differences in density depending on its exposure to areas where recreational fishing may be taking place. In addition, this density may be higher before the recreational fishing season, in late spring, and decrease in late summer.

Chapter IV

Vulnerability to being fish is a behaviour-related syndrome. The information related to this is increasing its importance in the management of fishery resources, especially in those related to recreational fishing. This vulnerability is related to different

intrinsic characteristics of the fish, but extrinsic characteristics such as socialization with other congeners and species or even the habitat itself may also be playing an important role.

Objectives: Using BRUV's we want to know how the habitat and the intra and inter specific social context affects the vulnerability of the *Serranus scriba* to being fished.

Hypothesis: The environment habitat and the local species (the fish community) would differ in their behaviours towards the bait at different levels and that could interfere in the vulnerability to angling of the *S. scriba*.

Chapter V

Exist an extensive bibliography describes that fish can exhibit different traits. In our case, the *Serranus scriba* has different life-history (e.g. growth; reproduction), behavioural (e.g. boldness) and physiological (e.g. metabolic rates) traits that makes it more or less vulnerable to fishing by anglers.

Objectives: Evaluate whether the quantity of eggs and their quality are related to the behavioural syndrome of being more or less vulnerable to fishing.

Hypothesis: One of the consequences of the different traits is to have different egg production between the vulnerable and non-vulnerable fish syndrome and this could be different due to the characteristics of the metabolism and consequently the release of different quantity and quality of eggs.

Chapter I - Estimating the density of resident coastal fish using underwater cameras: accounting for individual detectability

Reference

Follana-Berná, G., Palmer, M., Campos-Candela, A., Arechavala-Lopez, P., Diaz-Gil, C., Alós, J., Catalan, I., Balle, S., Coll, J., Morey, G., Verger, F., Grau, A., 2019. Estimating the density of resident coastal fish using underwater cameras: accounting for individual detectability. *Mar. Ecol. Prog. Ser.* 615, 177–188. doi:10.3354/meps12926

Chapter II - Fish density estimation using unbaited cameras: Accounting for environmental-dependent detectability

Reference

Follana-Berná, G., Palmer, M., Lekanda-Guarrotxena, A., Grau, A., Arechavala-Lopez, P., 2020. Fish density estimation using unbaited cameras: Accounting for environmental-dependent detectability. *J. Exp. Mar. Bio. Ecol.* 527, 151376. doi:10.1016/j.jembe.2020.151376

Chapter III - Mesoscale assessment of sedentary coastal fish density using vertical underwater cameras.

Authors

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Reference

Follana-Berná, G., Pablo Arechavala-Lopez, P., Ramirez-Romero, E., Koleva, E., Grau, A., Palmer, M. 2021. Mesoscale assessment of sedentary coastal fish density using vertical underwater cameras. Fish. Res. (Under review)

Abstract

Accurate and precise monitoring of absolute density (i.e., number of fish per area or volume unit) of exploited fish stocks would be strongly advisable for deriving the stock's status and for designing proper management plans. Moreover, monitoring should be achieved at relevant (i.e., large enough) temporal and spatial scales. This objective is particularly challenging for data-poor fisheries, as it uses to be the case of recreational fishing. Therefore, here, as a proof of concept, the feasibility of underwater video monitoring (vertical unbaited cameras) for estimating the absolute density of coastal sedentary fish species is demonstrated. The absolute density of a small serranid (*Serranus scriba*) has been estimated with suitable accuracy and precision alongside the south coast of Mallorca Island (nearly 100 km). Fish density ranged between 2 ind/km² and 59,115 ind/km². These large differences are explained by exposure to fishing, and by minor site-specificities of habitat and depth, all well within the previously reported environmental range of the studied species. Site-specific, seemingly long-term, effects of fishing are negatively correlated with fish density, but short-term effects (assessed by the interaction between exposure to fishing and before/after the season when recreational fishing accumulated at the studied area) were not detected. We suggest that the short-term effects of fishing may remain undetected because highly exploited sites could inhabit fish that are already non-vulnerable to fishing, irrespective of the short-term fishing pressure exerted. Such a process may explain some hyperdepletion patterns and should prevent the use of fisheries-dependent data for monitoring fish density.

Keywords

absolute density, unbaited cameras, recreational fishing, fisheries management.

Introduction

Proper assessment of population dynamics is essential for ensuring sustainable management and effective conservation of species and habitats (Milner-Gulland and Rowcliffe, 2007). Specifically, supplying accurate and precise monitoring of the absolute density (i.e., number of fish per area or volume unit) of exploited fish stocks is strongly advisable for deriving the stock's status and for designing proper management plans (Giacomini et al., 2020; Pauly et al., 2013). Nevertheless, biological reference points of stock assessment are usually defined using fishery-dependent data, in spite that it is well known that they are prone to bias (Alós et al., 2014, 2015a; Alós and Arlinghaus, 2013; Saul et al., 2020) and, thus, they may lead to inappropriate management decisions (Simmonds, 2007). In addition, wildlife monitoring should be achieved at relevant (i.e., large enough) temporal and spatial scales for adopting management decisions (Pollock et al., 2002).

These problems exacerbate in the case of recreational fishing (Post, 2013), about which there are concerns on its impact on fishery resources (Cooke and Cowx, 2004). Marine recreational fishing is one of the most extended leisure activities in coastal waters worldwide (Hyder et al., 2018; Post, 2013) and it is a particularly relevant activity along the Mediterranean coasts, where may represent around 10% of total catches, and where is involving a huge number of practitioners (Grau, 2008; Morales-Nin et al., 2015, 2005).

However, collecting data about recreational fishing efforts or catches and, most importantly, predicting the effects of recreational fishing on the population dynamics of the exploited species are particularly elusive tasks (Arlinghaus and Cooke, 2005; Radford et al., 2018).

Provided that underwater video techniques are increasingly used for monitoring reef fish, here we aim to demonstrate the feasibility of underwater video for estimating the absolute density of, as a proof of concept, a coastal fish species heavily exploited by recreational fishing. Underwater cameras are already providing an unprecedented amount of fishery-independent data (Mallet and Pelletier, 2014; Przeslawski and Foster, 2018; Sheaves et al., 2020). Their use is currently so widespread that underwater cameras are reshaping the way the marine realm is observed (Mallet and Pelletier, 2014; Sheaves et al., 2020).

The relative abundance indexes extracted from several camera settings have been extensively compared to each other and against underwater visual censuses and other methods (Watson et al., 2005). Unfortunately, these empirical comparisons evidenced that effective integration of relative abundance indexes from different monitoring methods is problematic, and it is better to use each method for each specific case (Cheal et al., 2021).

In contrast with those relative abundance indexes, several methodological advances for extracting absolute density (i.e., number of fish per area or volume unit) from fish counts per frame have been recently proposed (Abolaffio et al., 2019; Campos-Candela et al., 2018; Campos-Candela et al., 2019; Follana-Berná et al., 2020, 2019). However, these contributions are developing theoretical concepts, are computer-

simulated experiments focussing on statistical challenges (e.g., accuracy and precision) or deal with technical issues (e.g., fish detectability or device design), but a real-world demonstration of the feasibility of extracting fish density at field conditions and at a scale large enough for supporting management decisions is still lacking. Such a real-world demonstration is essential because, in spite that the density estimates obtained by these methodological advances seem unbiased and accurate (Abolaffio et al., 2019; Campos-Candela et al., 2018), there is still some debate on whether the sampling effort needed for achieving a target precision is affordable or not (Abolaffio et al., 2019; Campos-Candela et al., 2019). Thus, our primary aim is to demonstrate the feasibility of underwater cameras for estimating the absolute density at the mesoscale (near 100 km along the south coast of Mallorca Island) of a small serranid (*Serranus scriba*) exploited by recreational fishing (Dedeu et al., 2019).

Moreover, and as a proof of concept too, we evaluated the feasibility of the proposed framework for testing ecological hypotheses. Specifically, we evaluated the effects of three of the most typical drivers affecting coastal fish density: habitat type, depth, and fishing (Stoner, 2004). Concerning fishing, the putative short term effects (i.e., between seasons in the same year) have been discriminated from the site-specific effects (i.e., exposure to fishing based on the distance to harbours; March, 2014) by monitoring the same sites before and after the summer, which is when most of the recreational fishing activity accumulates in Mallorca (Cabanellas-Reboredo et al., 2014; March et al., 2014). The hypothesis of short-term effect is assessed by comparing the between-season differences in density along a gradient of fishing exposure (i.e., larger decreases in density are expected at sites more exposed to fishing), while fish average (across-seasons) density

is expected to be smaller at more exposed sites under the hypothesis of site-specific (i.e., plausibly long-term) effects.

Materials and Methods

Study area and sampling

To estimate the absolute density of *S. scriba*, 15 sites were sampled covering the south coast of Mallorca Island (Figure III—1 and Supplementary figure B-1).

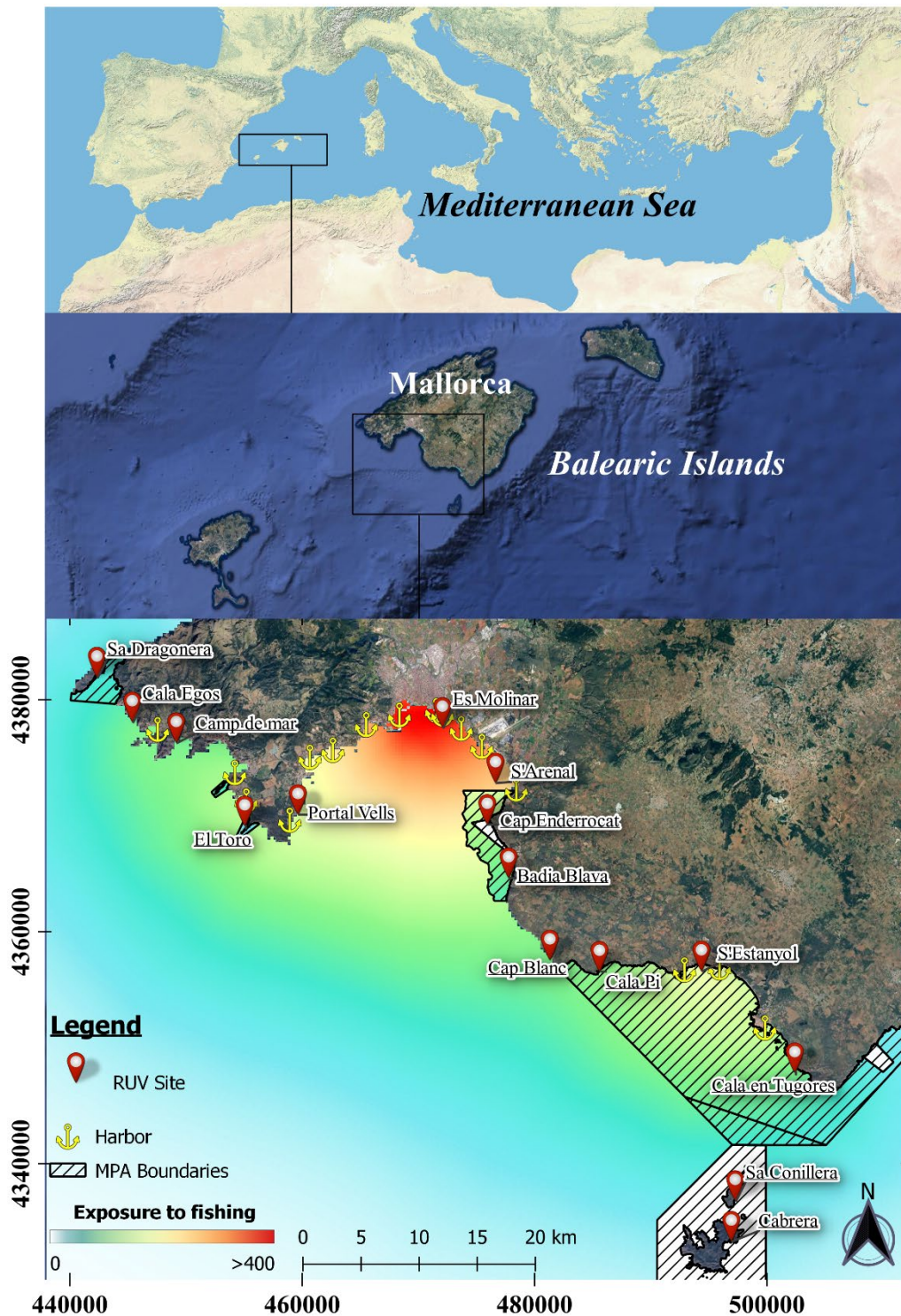


Figure III—1. Map with the location of each sample in the area of the coast of Mallorca. The anchors represent the presence of ports, the red buttons the location where cameras were

deployed, the polygons with lines represent the MPA's and the Exposure to fishing from white (no fishing exposure) to red (maximum exposure to fishing) .

The selected sampling sites were distributed along 100 km, and they display well-contrasted exposure to fishing and management strategies (e.g. from heavily exploited sites to marine protected areas, MPAs), and cover the full environmental gradient range inhabited by *S. scriba*: from rocky bottoms to seagrass meadows of *Posidonia oceanica*, and from the coastline to around 30 m depth (March et al., 2010).

At each sampling site, ten vertical underwater camera devices (Supplementary figure B-2) were randomly deployed within an area of approximately between 1 and 0.5 km² for assessing the variability of fish density at a short spatial scale. Camera sites were located on suitable habitat for *S. scriba*, and distances between cameras in the same Season were larger than 200 m to minimize between-cameras spatial autocorrelation (Chapter II; Follana-Berná et al., 2020). All the devices from a given site and season were deployed on the seabed in a single day and left from (approx.) 8:00 to 12:00 pm, which ensures that each device has been recording till the battery life lasted (about 3 h and 15 min).

As stated above, two samplings were completed at each of the 15 sites for assessing the short-term effects of exposure to fishing on fish density: late spring and late summer. This sampling design should provide overall 300 videos (15 sites, 10 cameras per site, and 2 seasons per site) but the actual number of videos analysed was 257 because of wrong deployments or technological problems with the cameras. Sampling dates and the coordinates of all the points where cameras were deployed are provided at the

repository (<https://doi.org/10.17632/8c5jwvkvsz.1>) (Follana-Berná, G. & Palmer, M. 2021).

The underwater camera device consists of a vertical structure with two action cameras Sony HDR AS50® separated each other by a distance of 20 cm and looking down with an angle of 45°. This design has been already successfully used for estimating the fish density of *S. scriba* (Chapter II; Follana-Berná et al., 2020). The device, built with PVC pipes, incorporates a counterweight at the base and a buoy at the top, which ensures its vertical position at any moment. The cameras were located at 150 cm from the base of the device (Supplementary figure B-2). The seabed area surveyed by a camera was 5.0 m² (Follana-Berná et al., 2020).

The videos were manually examined by an observer, following a previously developed and tested protocol (Chapter II; Follana-Berná et al., 2020). Briefly, the first minute after the device landing on the seafloor was discarded to avoid any abnormal fish behaviour. Then, the number of individuals in one single frame was counted every 120 seconds. The average number of frames counted per video was 90. Previous trials ensured that temporal autocorrelation between frames is not relevant at this counting frequency. In practice, the reading was made easier by using video viewing software that jumps from the actual target frame to a few seconds just before the next target frame. Fish movement largely facilitated fish detection during these few seconds but only those fish that are strictly present at the target frame were counted.

Explanatory variables: Exposure to fishing, habitat, and depth

Distance to ports has been used as a proxy of commercial fishing effort for explaining the spatial distribution of fishing effort (Caddy and Carocci, 1999). Accordingly, and following the rationale developed by (March et al., 2014), the variable *exposure_to_fishing* was defined based on a gravity model of the distance from all the ports on the south coast of Mallorca to each of the points where the cameras were deployed. These distances were weighted by the number of sport fishing licenses of each port (years 2014 to 2016, data provided by Direcció General Pesca i Medi Mari, Govern de les Illes Balears). In addition, this index was also weighted by the scaled number of days that recreational fishing is allowed at a given site. That is, this additional weight is zero at no-take marine reserves, one at fully open sites, or something between at partial marine reserves, depending on the number of days per week that fishing is allowed.

$$Exposure\ to\ fishing_i = \left(\sum_{j=15} Fishing\ Licences_j / Port\ Distance_{j \rightarrow i} \right) *$$

$$MPA's\ Fishing\ days_i \quad \textbf{Equation III-1}$$

Where *i* is the site where a camera has been deployed and *j* is each of the ports. The *costDistance* function from the *gdistance* package (van Etten, 2017) was used to estimate the least-cost distance of each sampling site to each port.

As stated above, sea bottom type and depth are also expected to drive the density of most coastal fish. The *depth* of each sampling location was extracted in-situ using the boat's probe. Sea bottom type at the specific point where a camera device was deployed was quantified using the percentage cover of three types of substrate (Follana-Berná et al., 2020): (1) percentage of patches with sand to gravel; (2) percentage of rocks or rocky

patches with many crevices and sharp slope changes, with or without small-sized algae; and (3) percentage of seagrass. These cover percentages were transformed according to Aitchison (1983). Finally, a Principal Component Analysis was completed on the transformed percentages and the PCA's scores on the two resulting axes (*habitat_1* and *habitat_2*) were used as explanatory variables summarizing the habitat characteristics.

Modeling fish density

One of the main challenges for translating fish count per frame into absolute abundance is to properly deal with environmental dependencies of detectability ($P_{\text{detection}}$, the probability of counting a fish that is actually within the surveyed area by the camera). Moreover, uncertainty in the detectability estimation must be properly propagated to the precision of density estimates. In the case of *S. scriba*, detectability has been previously estimated to be 0.82, with a 95% Bayesian credibility interval between 0.52 and 0.99 (Follana-Berná et al., 2020). Moreover, $P_{\text{detection}}$ has been demonstrated to be independent of the sea bottom characteristics, at least within the environmental gradient considered (Follana-Berná et al., 2020). $Counts_{i,j}$ (the number of fish counted for the i th camera device at the j th frame, where $i = 1$ to 257 videos and $j = 1$ to approx. 90 frames per video) has been assumed to be Poisson distributed as (Campos-Candela et al., 2018; Follana-Berná et al., 2019; Follana-Berná et al., 2020):

$$Counts_{i,j} \sim \text{Poisson}(Area_camera * Density_i * P_detection) \quad \text{Equation III-2}$$

where $Density_i$ is the fish density around the i camera and $Area_camera$ is the area surveyed by the camera, which has been estimated with negligible error (5.0 m²) obtaining

the density of fish per square meter. Fish density was modelled as a linear combination (at the log scale) of the *exposure_to_fishing* index describe above, the two quantitative variables describing habitat (*habitat_1* and *habitat_2*), and *depth*. The correlations between the four explanatory variables considered were small (the largest Pearson's r^2 was 0.06), thus collinearity problems are not expected. A quadratic term has been included for *habitat_1*, *habitat_2*, and *depth* to account for possible unimodal responses. Moreover, the *season* was also included in the model allowing for (1) different intercepts (between season differences) and (2) different slopes for the fishing effort at late spring *versus* late summer (i.e., an interaction term). Finally, two random effects were considered. First, fish density at the point where a camera device has been deployed was allowed to be normally distributed (at the log scale) around the site mean, with a common standard deviation (σ_{camera}). Second, the model intercept for a given site was allowed to be normally distributed (at the log scale) around a general intercept with a given standard deviation (σ_{site}), thus the latter random effect is accounting for the between-site variability that is not explained by the fixed factors (*exposure_to_fishing*, *habitat type*, and *depth*).

The parameters of this model were fitted using a Bayesian approach. Samples from the joint posterior distribution for fish density and the slopes and intercepts of the model given the data (fish counts) were obtained using STAN and the *rstan* library (Stan Development Team, 2020) of the R package (R Core Team, 2017). Uncertainty in *P_detection* was injected in the model after adjusting the posterior distribution reported by (Follana-Berná et al., 2020) to a beta distribution, which was done using the *fitdistrplus* library (Delignette-Muller and Dutang, 2015) from the R package. Any additional detail on the model structure has been made available in an R script provided at the repository <https://doi.org/10.17632/8c5jwvkvsz.1> (Follana-Berná, G. & Palmer, M. 2021). The data

counts and explanatory variables are available too. Four chains were run. Chain convergence was assessed by visual inspection of the chains and was evaluated using the Gelman-Rubin statistic (Gelman et al., 2015). Posterior distributions of the model parameters were estimated by 12,000 valid iterations after appropriate warm-up (the first 1,000 iterations were discarded).

Results

The mean depth in meters of all sampling sites was 13.3 ± 5.1 m. The depth range of the deployment points of the camera devices ranged from 2 m to 32 m (Figure III—2).

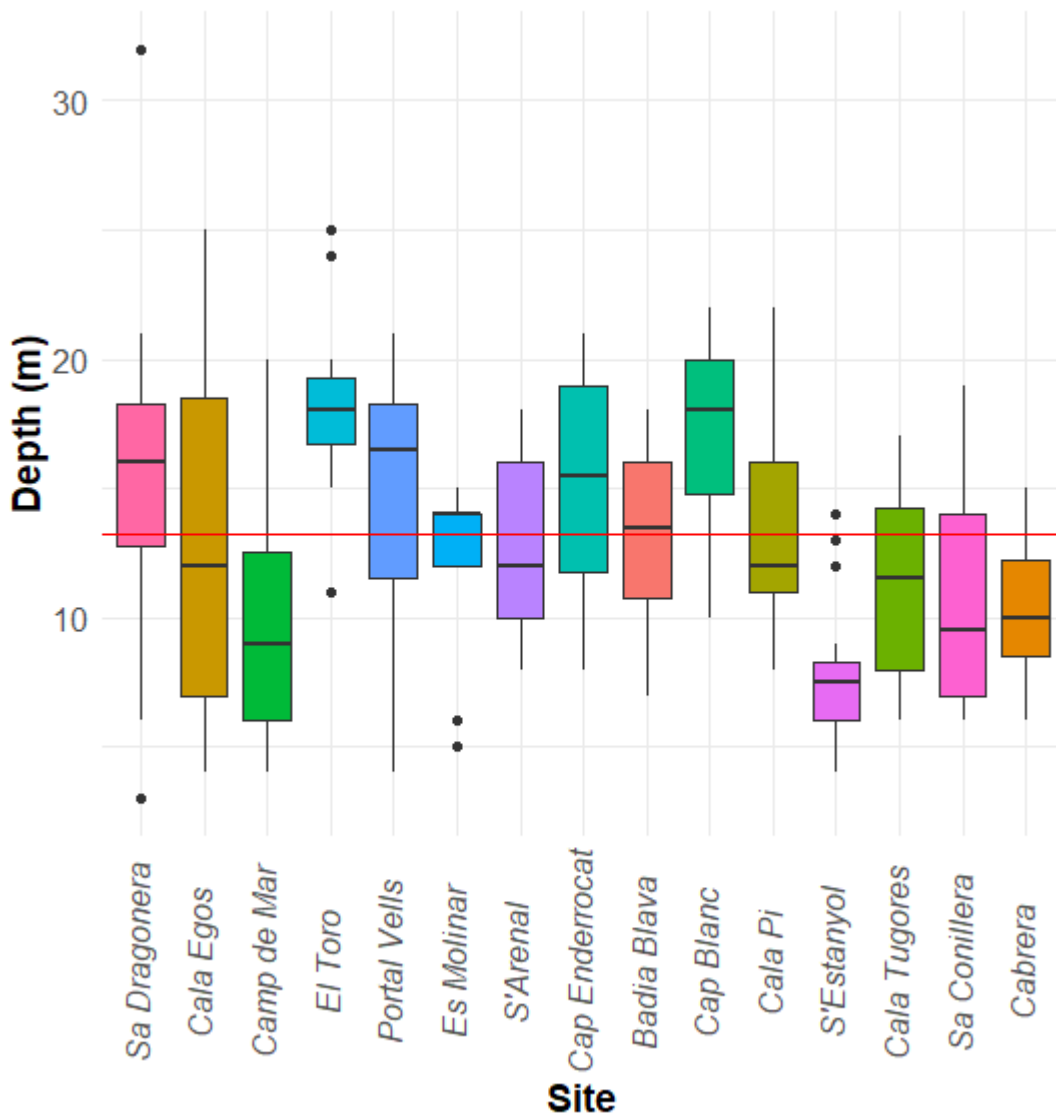


Figure III—2. Depth between-site boxplot at camera level. The line in the middle of the box indicates the median; the upper and lower limits of the box represent the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

The *exposure_to_fishing* index varied among sampling sites, reaching the highest values close to marinas (e.g., *Es Molinar*, *S'Arenal*; Figure III—3) and the lowest values at MPAs and sites far from any harbour (i.e. *El Toro*, *Cap Enderrocat*, *Cabrera*, *Sa Conillera*).

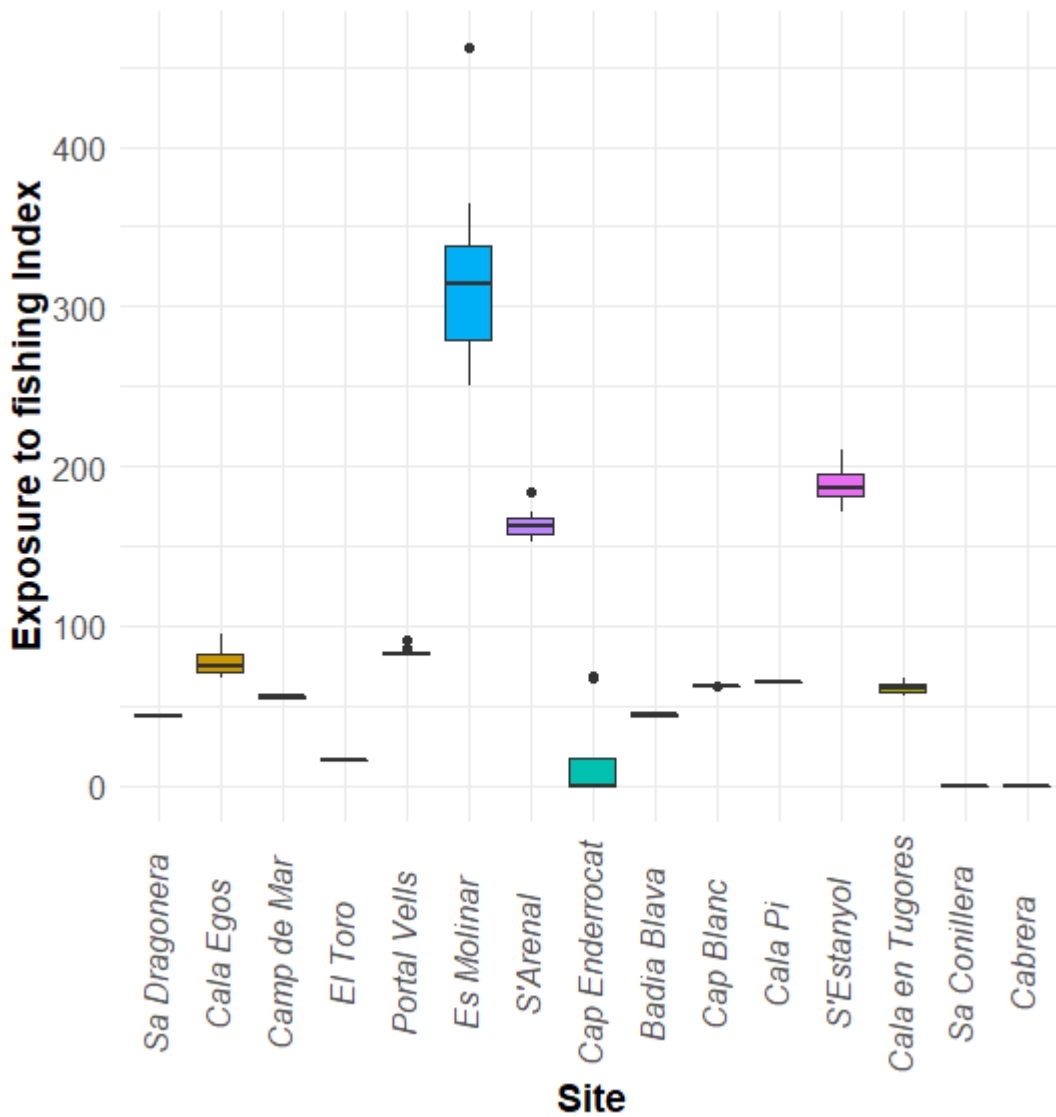


Figure III—3. Exposure to fishing between-site boxplot at camera level. The line in the middle of the box indicates the median; the upper and lower limits of the box represent the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

Regarding the habitat, the 257 sampling locations were classified according to the bottom coverage (%), which after transformation and factorization (i.e., PCA) resulted in two axes (*habitat_1* and *habitat_2*) that explain the 57% and the 43% of the variance (Figure III—4).

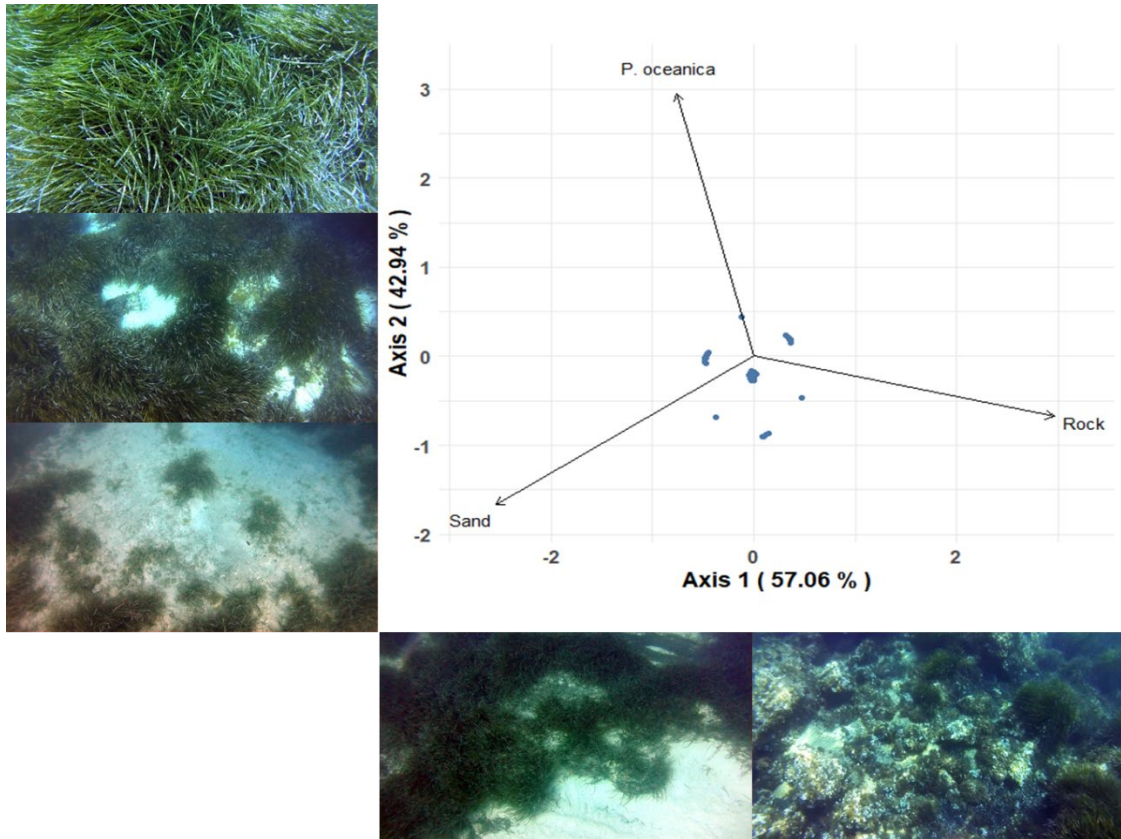


Figure III—4. PCA habitat scores. The images of the Axis 1 is a sample of the maximum and minimum habitat axis score. The same for the axis 2 but the middle image is the median score.

Both axes were used as explanatory variables (Figure III—5). The axis 1 explains the gradient between sand (minimum score = -0.4797) to rock (maximum score = 0.4729). The axis 2 is related with the coverage of *P. oceanica*. Sites with scores close to the maximum (0.4369) display covers close to 100%, while *P. oceanica* is absent at sites with score close to the minimum (-0.8996).

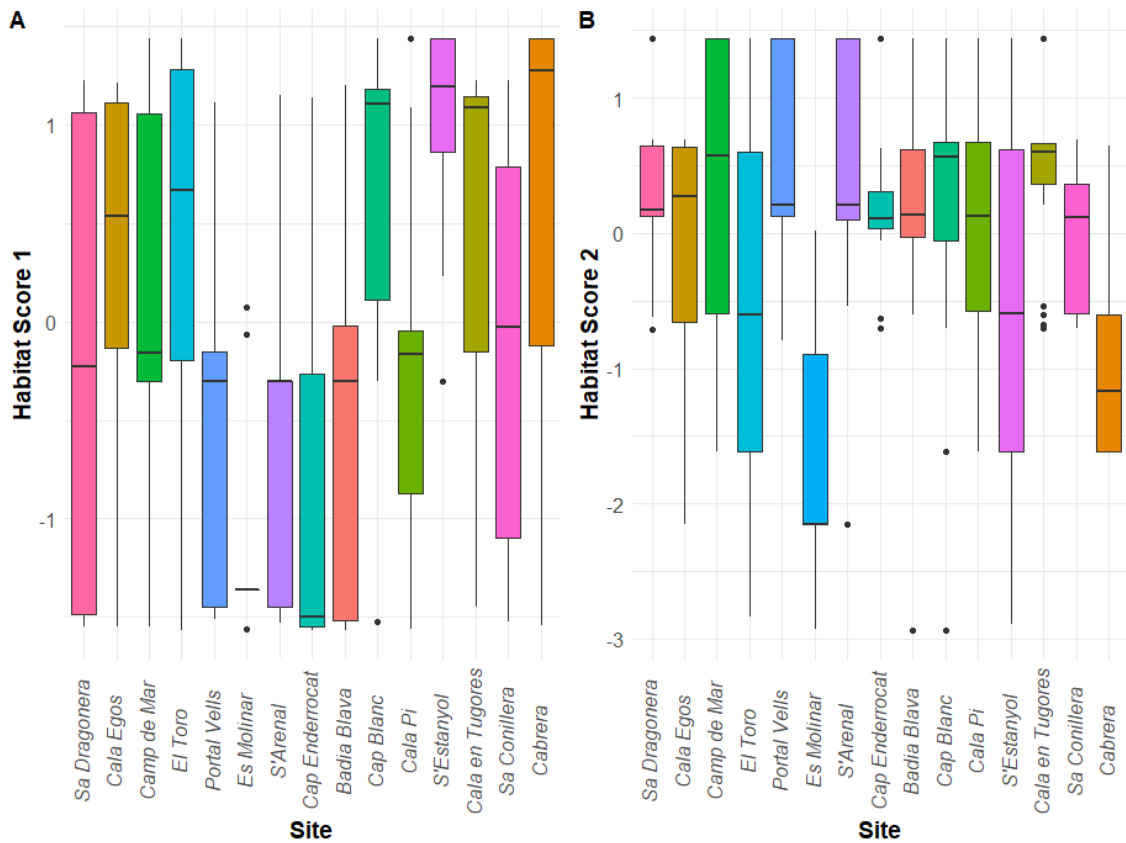


Figure III—5. Habitat scores (A) axis 1 and (B) axis 2) between-site boxplots at camera level. The line in the middle of the box indicates the median; the upper and lower limits of the box represent the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

The parameters of the statistical model detailed above given the counted number of fish per frame have been successfully estimated (no divergences, E-BFMI indicated no pathological behaviour, $Rhat$ was always between 0.998 and 1.002; the effective number of samples was always larger than 2,000). Regarding the estimated densities of *S. scribe* (Figure III—6), the highest absolute densities were found in *Cabrera* (median: 14,294 ind/km²; 95% Bayesian Credibility Interval, 95%BCI: 8,229 to 29,238 fish/km²),

followed by *Cap Blanc* (4,932 fish/km², 95%BCI: 2,949 to 9,629 fish/km²) and *El Toro* (4,844 fish/km², 95%BCI: 2,622 to 9,990 fish/km²). The lowest absolute densities were expected in *Es Molinar* (299 fish/km², 95%BCI: 36 to 1,640 fish/km²), followed by *Portals Vells* (659 fish/km², 95%BCI: 271 to 1,534 fish/km²) and *S'Arenal* (811 fish/km², 95%BCI: 269 to 2,550 fish/km²) (Figure III—6).

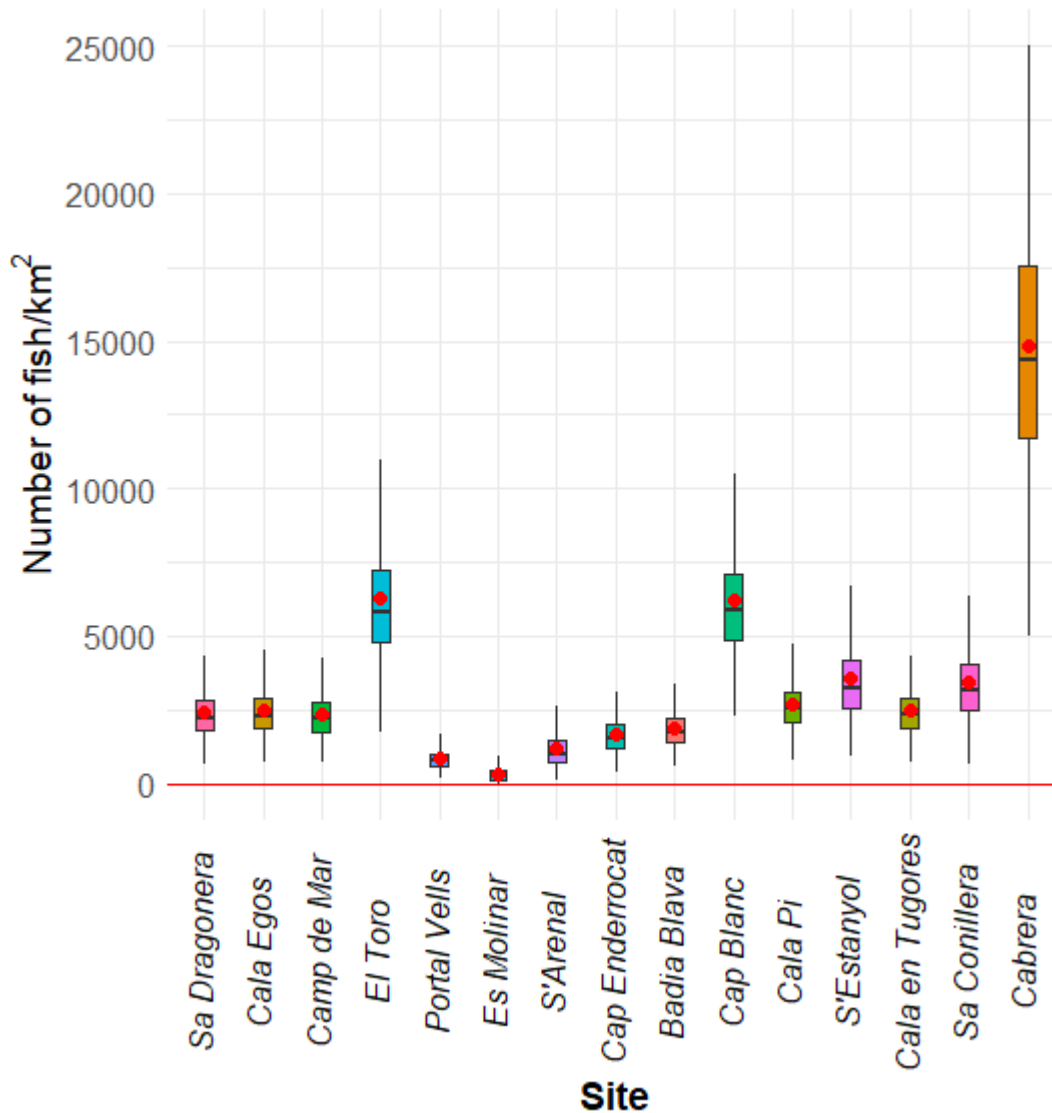


Figure III—6. Boxplot with estimated fish density (ind/km²). The red dot indicate the mean. The line in the middle of the box indicates the median; the upper and lower limits of the box represent

the interquartile range and whiskers represent values at 1.5 times the interquartile range of the box.

Concerning the effects included in the statistical model, the intercepts for late spring and late summer did not differ between each other (95%BCI includes zero; Figure III—7), suggesting that the average density across sites remained the same between the two seasons of a given year.

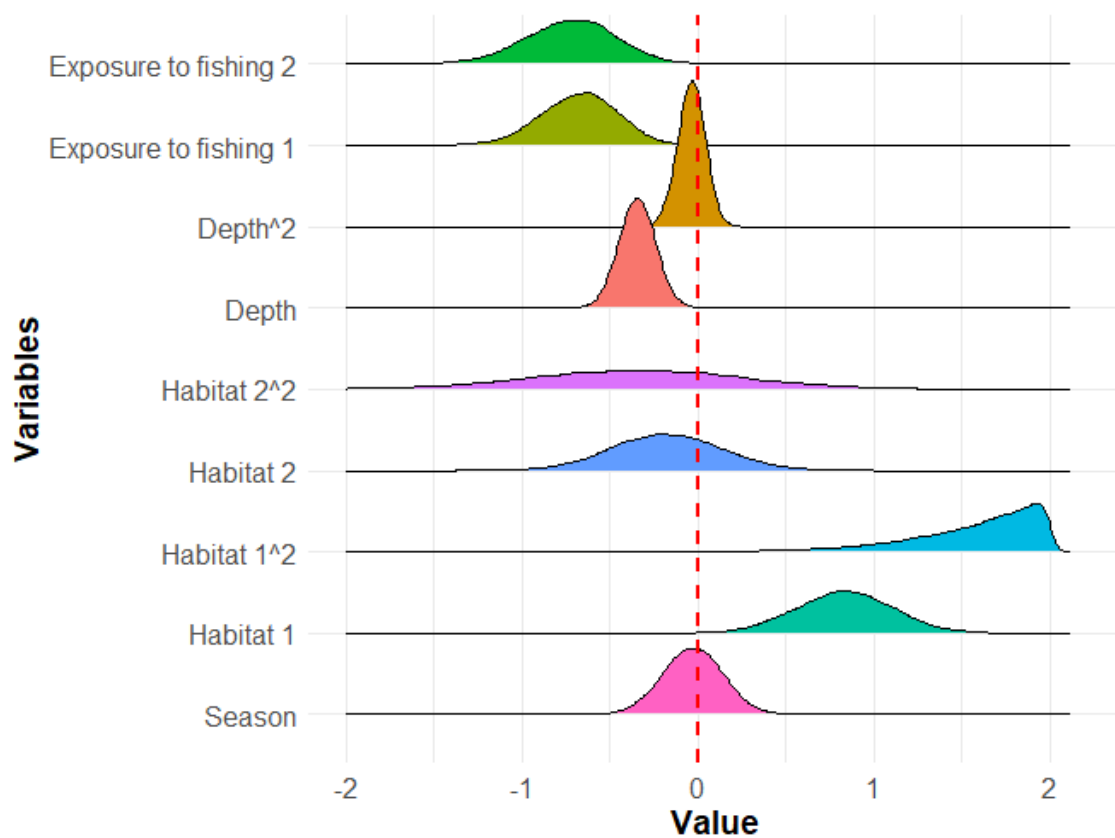


Figure III—7. Model effect (showing whether it includes zero or not) of different fishing and temporal seasons, as well as habitat parameters, on *S. scriba* densities surveyed with vertical RUVs.

However, relevant effects (95%BCI does not include zero) on fish density were detected for the slope of the habitat scores at the first dimension and its quadratic term (i.e., the response to the habitat gradient seems to be an unimodal pattern). The slopes of the habitat scores at the second dimension were not relevant. According to these results, the worse habitat score for *S. scriba* along the habitat's gradient sampled (Figure III—4 and Figure III—5), were -0.37 (95%BCI: -0.94 to 0.11), which corresponds to uniform *Posidonia* meadows (Figure III—4). Fish density is expected to increase toward *Posidonia* meadows mixed with either, rocks or sand (i.e., toward more heterogeneous habitats; the expected patterns when one explanatory variable by turn is allowed to change along the actual gradient while the other are kept constant at its average value are provided at Figure III—8A).

Similarly, there were relevant effects on fish densities of the season-specific slopes of *exposure_to_fishing* (Figure III—7). In both seasons, the larger the *exposure_to_fishing* index, the smaller the fish density is expected to be, which suggests that fishing is reducing the site-specific (i.e., averaged across seasons) fish density (Figure III—8B). Interestingly, 95%BCI of the difference between these two slopes does include zero (Figure III—7), which strongly suggests that the interaction between *season* and *exposure_to_fishing* was not relevant and, thus, no short-term (between seasons) effects of fishing was detected. Finally, relevant effects (95%BCI does not include zero) on fish density were also detected regarding the slope related to *depth*. In that case, provided that the effect of the quadratic term was not relevant, the existence of an optimal depth within the sampled depth gradient (Figure III—2) was not supported; thus, the deeper a site, the smaller the fish density is expected to be (Figure III—6, and Figure III—8C).

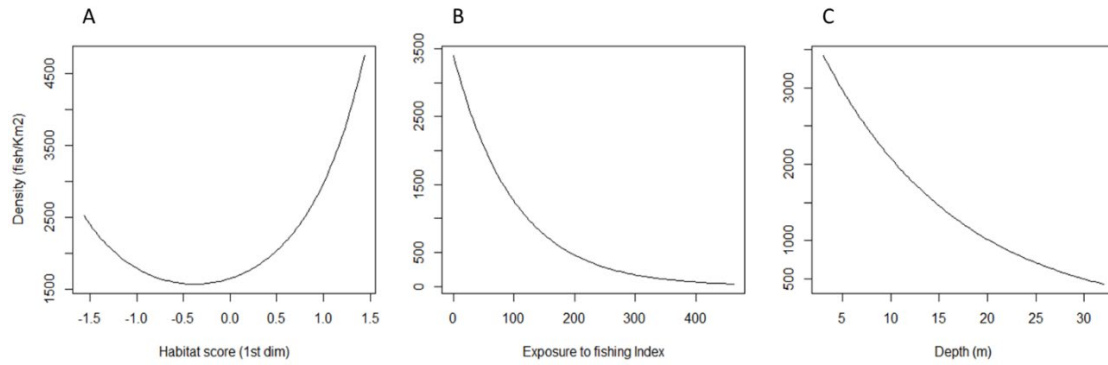


Figure III—8. Description of relevant effects (95% BCI does not include zero) on fish density. Average value of the expected patterns for A) Habitat score 1, B) Exposure to fishing Index and C) Depth

Discussion

The feasibility of underwater video monitoring for estimating the absolute density of coastal fish species has been demonstrated. The absolute density of a small serranid (*S. scriba*) has been estimated with suitable accuracy and precision alongside the south coast of Mallorca Island (nearly 100 km). Therefore, the proposed sampling framework arises as a realistic alternative for long-term monitoring of coastal fish at temporal and spatial scales that are relevant for adopting management decisions (i.e., at the mesoscale). In addition, the capability of the proposed framework for testing ecological hypotheses has been demonstrated too. Certainly, the effects of habitat, fishing, and depth on coastal fish density are well known (Gerald et al., 2019). Thus, the relevance here is that the proposed framework is fully capable of generating the data needed for testing any ecologically sound hypothesis with enlarged statistical power and at an affordable cost.

The proposed framework implies monitoring with vertical unbaited cameras, which seems to be robust against the biases affecting other fishery-dependent sampling methods and other camera settings. The advantages and limitations of the vertical unbaited cameras are compared against the two fishery-independent methods most commonly used for monitoring coastal fish at similar temporal and spatial scales (baited cameras and underwater visual censuses; Table III-1). Cameras with horizontal field views are not explicitly included in Table III-1 because irrespective of using bait or not, they suffer from the problem that measuring the area surveyed is elusive (Sheaves et al., 2020) and that some fish may remain occluded by rocks or any other item. Certainly, the area surveyed by a vertical camera can experience slight variations depending on the substrate roughness and the precision of the area limits in a belt census would depend on the diver training, but these uncertainties are negligible when compared with those from horizontal cameras. Apart from that, the advantages and limitations of horizontal cameras are those linked with the use of bait or not (Table III-1).

Table III-1. *Comparison between Underwater visual censuses and Cameras (Baited and Unbaited)*

	Visual censuses	Baited cameras	Unbaited cameras
Risk for the observer	Medium-High	No	No
Suitable at extreme habitats	No	Yes	Yes
Disturbances to fauna/habitat	Soft	Soft	Negligible
Disturbances to fish behaviour	Yes(diver's presence)	Yes (bait)	Soft.
Absolute density	Yes, after estimating detectability	No	Yes, after estimating detectability
Accuracy	Acceptable. Some species can be underestimated (fear) or overestimated (attraction)	Biased	Acceptable. Cryptic, static species can be underestimated.
Precision	Acceptable but at a larger cost	Unknown	Acceptable
Review/check is possible	No	Yes	Yes
Appropriate at a long temporal scale	Yes, but at a larger cost	Yes	Yes
Appropriate at a long spatial scale	Yes, but at a larger cost	Yes	Yes
Cost: Initial investment	High	Medium and falling	Medium and falling
Cost: Equipment maintenance	High	Medium	Medium
Cost: Training	Very high	Medium	Medium
Staff cost per sample	High	Medium	Medium
Cost: Post-processing	Low	High, but expected to drop with Deep Learning algorithms	High, but expected to drop with Deep Learning algorithms

Some generic advantages of cameras over visual censuses are the reduced risks for the staff (divers), and the wider gradient of extreme habitats that can be safely sampled (Mallet and Pelletier, 2014). Cameras also allow re-checking of the interpretation of the videos (fish counts and species identification). Cost is certainly more difficult to compare, but overall the initial investment of the divers' equipment and its maintenance seems larger when compared with action cameras, which are quickly becoming more affordable and with better quality. Thus, the number of cameras, the deployment time, or the area surveyed by a camera will not be an economic limiting factor in the near future (Aguzzi et al., 2020b, 2020a, 2015; Campos-Candela et al., 2019; Matabos et al., 2015, 2014; Struthers et al., 2015). The training cost of the divers and the staff cost per sample (fieldwork) is larger in comparison with cameras.

Both, visual censuses and vertical unbaited cameras can produce unbiased estimates of absolute fish density after species-specific fish detectability has been estimated. Detectability should preferably be estimated in an independent field survey (Follana-Berná et al., 2019; Follana-Berná et al., 2020; MacNeil et al., 2008; Pollock et al., 2002). Detectability estimation is species-specific and may need ad-hoc solutions (Follana-Berná et al., 2020) but it is feasible to model environmental dependencies (Follana-Berná et al., 2020; Follana-Berná et al., 2019) and, thus, properly account for potentially confounding effects as, for example, those related with water turbidity (Figuroa-Pico et al., 2020). Similarly, the area surveyed by visual censuses and vertical unbaited cameras can be measured with no or small error, thus allowing to link the count to an area unit. As stated above, this is a major handicap of any camera setting with a horizontal field view.

Both visual censuses and vertical unbaited cameras can theoretically reach any target precision, but the number of samples needed may be unaffordable (Abolaffio et al., 2019). Nevertheless, this problem exacerbates in the case of visual censuses because the cost per sample is larger. It should be noted here that the number of counted fish per frame follows an ergodic process concerning time and space, provided that fish density is constant at the surveyed temporal scale (Campos-Candela et al., 2018). This assumption seems to meet at the one-day temporal scale of sampling used here and for most of the coastal fish displaying a home-range pattern of space occupation (Alós et al., 2016; Arechavala-Lopez et al., 2019; Follana-Berná et al., 2020; Jadot et al., 2006; Jones, 2005; March et al., 2010; Palmer et al., 2011). Therefore, the surface sampled by belt visual censuses (typically, in the range of 1,000 m²/day, assuming 4 censuses per day of 50 m long and 5 meters wide census; (Follana-Berná et al., 2019) may be even smaller than the area surveyed by the camera settings used here (4,500 m²/day: 90 frames per camera, 10 cameras, and 5.0 m²). Computer simulation experiments suggest that the later sampling setting ensures a target accuracy of about 90 % (Campos-Candela et al., 2018; Follana-Berná et al., 2020b; Follana-Berná et al., 2019). Therefore, the use of vertical unbaited cameras emerge as a plausible method for monitoring fish abundance at large spatial (as reported here) or temporal scales (e.g., permanent underwater observatories (Aguzzi et al., 2020; Matabos et al., 2014)).

The use of baited cameras is certainly widespread but it is also well known that the fish counts provided by this method are biased (Cheal et al., 2021). To see more fish does not mean that the counted fish reflects the actual density. Bait interferes with fish behaviour and the attraction strength may depend on the bait characteristics (Ghazilou et al., 2016), the hydrography or dynamics of the odour plume (Taylor et al., 2013), of

species-specificities (e.g., species-specific olfactory capability; carnivores versus herbivores) or even individual-specificities (competitive interactions at either within- and between-species, satiety, or many other processes) (Bassett and Montgomery, 2011; Stoner, 2004). Certainly, some interesting attempt for modelling the attraction dynamics have been made (Dunlop et al., 2015; Vabo et al., 2004), but the multiple processes involved and its complexity make very difficult to generalize a method for linking fish density with the fish counts recorded by a baited camera. Unbaited cameras and UVCs can also trigger some species- or individual-specific abnormal behaviour (e.g., diver presence may trigger flight or hiding behaviour (Pierucci and Cózar, 2015; Trevor et al., 2000)), but the responses would not be comparable with those of the baited cameras. An extreme case of potential bias could be the permanent underwater observatories (e.g., https://imedea.uib-csic.es/sites/sub-eye/home_es/) that may act as artificial reefs (Aguzzi et al., 2020). These potential drawbacks should be further and carefully analysed but they are expected to be minimized with, for example, the sampling settings adopted here (discarding the few minutes of video after the device landing on the seafloor and sampling during a few hours only).

Video post-processing has been adduced as one of the major disadvantages of cameras in front of censuses (Mallet and Pelletier, 2014). However, Deep Learning algorithms (Connolly et al., 2021; Ditria, 2020; Salman et al., 2019; Tabak et al., 2019) for automatically extract information from fish images and videos are currently exploding (Álvarez-Ellacuría et al., 2019; Connolly et al., 2021; Martorell-Barceló et al., 2021; Moen et al., 2018). Some operational (i.e., real-time) applications for counting fish maybe even plausible soon (Meng et al., 2018), which may circumvent the bottleneck of memory

for video storage. Thus, it is expected that post-processing time and effort may drop in the near future.

As stated above, absolute density, in addition to the obvious advantages when modelling population dynamics for informing management decisions, allows proper comparison between studies (Cheal et al., 2021). However, if fish detectability is not estimated, such a comparison should be done with some caution. Nevertheless, the figures provided by underwater censuses at the same region (Balearic Islands) seem comparable with the figures reported here, which suggest a high fish detectability of underwater censuses. For example, the densities of *S. scriba* in the northern coast of Mallorca Island (5,000 ind/km²), in the south-western coast of Mallorca (11,300 to 18,500 ind/km²) or *Cabrera* (at the south of Mallorca; from 6,400 to 22,400 ind/km²; Deudero et al., 2008; Ordines et al., 2005; Reñones et al., 1997) fall within the densities estimated here. Similarly, the environmental preferences deduced from these studies fully agree with those reported here (e.g., *S. scriba* seems more abundant at shallow, heterogeneous *Posidonia* meadows), excepting in the case of Deudero et al., (2008), who suggest that the abundance of *S. scriba* is larger at deeper sites. The presence of rocks *per se* seems not enough for enhancing density because *S. scriba* inhabits artificial reefs on seagrass meadows but is absent from the artificial reefs located at nearby sandy areas (Coll et al., 1998).

In the same line, the abundance and environmental preferences of *S. scriba* estimated from visual censuses at other Mediterranean regions are similar to those reported here. At the Western Mediterranean (Serra Gelada: between 2,000 to 14,500 ind/km² (Arechavala-Lopez et al., 2008) and Cabo de Palos: 10,200 ind/km²; (García-

Charton and Pérez-Ruzafa, 2001). At the Adriatic Sea (between 4,000 and 27,000 ind/km² at shallow rocky algal reefs, whereas lower density was reported at uniform *P. oceanica* meadows (Bonaca and Lipej, 2005). At the South-Easter coasts of Italy (27,500 ind/km² at *P. oceanica* meadows and 17,500 ind/km² at other rocky-algal reefs (Guidetti, 2000)) or at the Central Aegean Sea, where *S. scriba* display close habitat preferences to those reported here (Giakoumi and Kokkoris, 2013). Interestingly, also in agreement with the results reported here, *S. scriba* densities at marine protected areas seem larger than those from non-protected areas (Guidetti et al., 2005).

The between-site variation reported here is well explained by the three explanatory variables considered (season, exposure to fishing, depth, and habitat characteristics). The sites with the highest density of *S. scriba* densities (i.e. *Cabrera*, *El Toro*, and *Cap Blanc*) display large patches of suitable habitats and experience no or very low fishing (Figure III—3, Figure III—4, Figure III—5). Recreational fishing is banned at *Cabrera* and limited at *El Toro* (partial MPA but far from any recreational fishing port) and *Cap Blanc* (open site to fishing but far from any port). Sites with intermediate density display either, low exposure to fishing or a larger patches of suitable habitat for *S. scriba*. In the case of the MPA at *Cap Enderrocat*, the large number of harbours and marinas at the Palma Bay may counteract the soft fishing limitations (fishing is allowed 4 days per week in most of the protected areas). The relatively low density estimated at *Sa Dragonera* deserves special attention because it is environmentally suitable for *S. scriba* but it is submitted to a relatively important recreational fishing. However, this area has been recently declared as MPA (in 2019), just before the fieldwork reported here was completed. Therefore, this site offers an unique opportunity for monitoring fish density in the next years and testing the effects of the establishment of the new fishing limitations.

Finally, the smallest densities were found at sites displaying both, a smaller proportion of optimally suitable habitats (heterogeneous *P. oceanica* meadows) and a larger recreational fishing (*Es Molinar* and *S'Arenal*).

The data reported here clearly support that sites with less fishing support larger fish densities. The correlational nature of this study precludes to explicitly suggest a cause-and-effect relationship, but the same pattern has been repetitively described at the same area and for the same species (Alós and Arlinghaus, 2013; March et al., 2014). Nevertheless, the sampling plan was specifically designed for discriminating short term effects (i.e., between seasons in the same year) from site-specific effects (i.e., long-term exposure to fishing) by monitoring the same sites before and after the summer, which is when most of the recreational fishing activity accumulates in Mallorca (Cabanellas-Reboredo et al., 2014; March et al., 2014). Therefore, short-term effects can be assessed by comparing the between-season differences in density along a gradient of fishing exposure (i.e., larger decreases in density are expected at sites more exposed to fishing). As stated above, the hypothesis of site-specific, long-term effects of fishing seems supported by the results, but no short-term effect has been detected. Several plausible explanations may be adduced. For example, the few remaining fish at heavily exploited sites may be almost invulnerable, thus the number of fish in those sites remains constant after the increase of the fishing pressure during the summer. The existence of a spatial pattern in vulnerability (fish are less vulnerable along a gradient of fishing) has been already described for the same species and area (Alós et al., 2015b) and should be a note of caution against the use of catch-per-unit-effort (i.e., fishery-dependent data) as a surrogate of fish abundance (Alós et al., 2019; Monk et al., 2021) because hyper-depletion

processes may give the wrong impression that fish abundance is smaller than actually is (Ahrens and Walters, 2005; Hilborn and Walters, 2013).

In summary, the results reported here suggest that fish monitoring with vertical unbaited cameras at large spatial and temporal scales is a reliable alternative in the near future. Baited cameras do not seem a reliable alternative for monitoring absolute density while the dynamic of the attraction was better understood and modelled. The proposed monitoring framework may be strongly benefited from the complementary role of diver's censuses but the combination of underwater cameras and artificial intelligence may represent a unique opportunity for a qualitative jump in the way marine wildlife is observed.

Acknowledgments

This work was funded by R&D project PHENOFISH (ref. CTM2015-69126-C2-1-R; MINECO) and the CLOCKS R&D Project (Grant num. PID2019-104940GA-I00; MICINN). This work is a contribution of the Joint Associated Unit IMEDEA-LIMIA. GFB was supported by a Spanish Ph.D. fellowship (FPI-INIA) from the National Institute for Agricultural and Food Research and Technology (INIA). PAL was supported by a post-doctoral grant (Juan de la Cierva Incorporación; IJCI- 2015-25595) from the Spanish Ministry of Economy, Industry, and Competitiveness. We would like to thank Joint Associated Unit IMEDEA-LIMIA staff members for helping with the surveys. Permits were received from the Cabrera Archipelago National Park and Direcció General de Pesca

i Medi Marí (Govern de les Illes Balears), the authors thank both organizations for allowing us to conduct this work.

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Chapter IV - Environmental and social effects on fish vulnerability to angling.

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Follana-Berná, G., Palmer, M., López-Aguilar, M., Grau, A., Arechavala-Lopez, P. 2021. Influence of environmental and social interactions on fish vulnerability to angling. Fish. Res. (Under review)

Abstract

Proper assessment of the potential effects of recreational fishing on fishery resources implies not only monitoring fishing effort but also a better understanding of the factors affecting the probability of capture (i.e., fish vulnerability). Multiple interrelated processes (those related with (1) the internal state of the fish, with (2) the fish-gear encounter processes or with (3) the gear specificities) have been suggested to shape the odds that a given fish can be captured or not in a given moment and at a given site. Here we explore the correlational patterns of a vulnerability surrogate (latency to bite, or the time a fish takes to attack the bait) with a number of potential explanatory variables that are related with most of the processes that has been proposed as vulnerability triggers, placing special stress in evaluating the role of social (i.e., between-fish) interactions. As a case study, we focused in *Serranus scriba*, an abundant, small-sized, carnivorous species that is a common target of recreational fishers in Mallorca. After deploying 138 underwater cameras at 15 locations covering all the South coast of Mallorca (i.e., covering all the environmental gradient inhabited by the species, and including marine protected areas and heavily fishing-exploited sites), we screened more than 2,500 minutes of video recordings, showing a device that emulates the most used hook-and-line configuration in Mallorca. The time between an individual of *S. scriba* appear in the scene and it, eventually, baits the hook (i.e., the latency time to bite) were recorded for 386 fish. The results showed that the larger the biting rate of other fish (any species) or the larger the number of *S. scriba* in the scene, the shorter the latency time to bite is. Contrasting, the larger the number fish around the bait but not interacting with it, the longer the latency time is. Habitat specificities are also affecting the latency time to bit of *S. scriba*, which

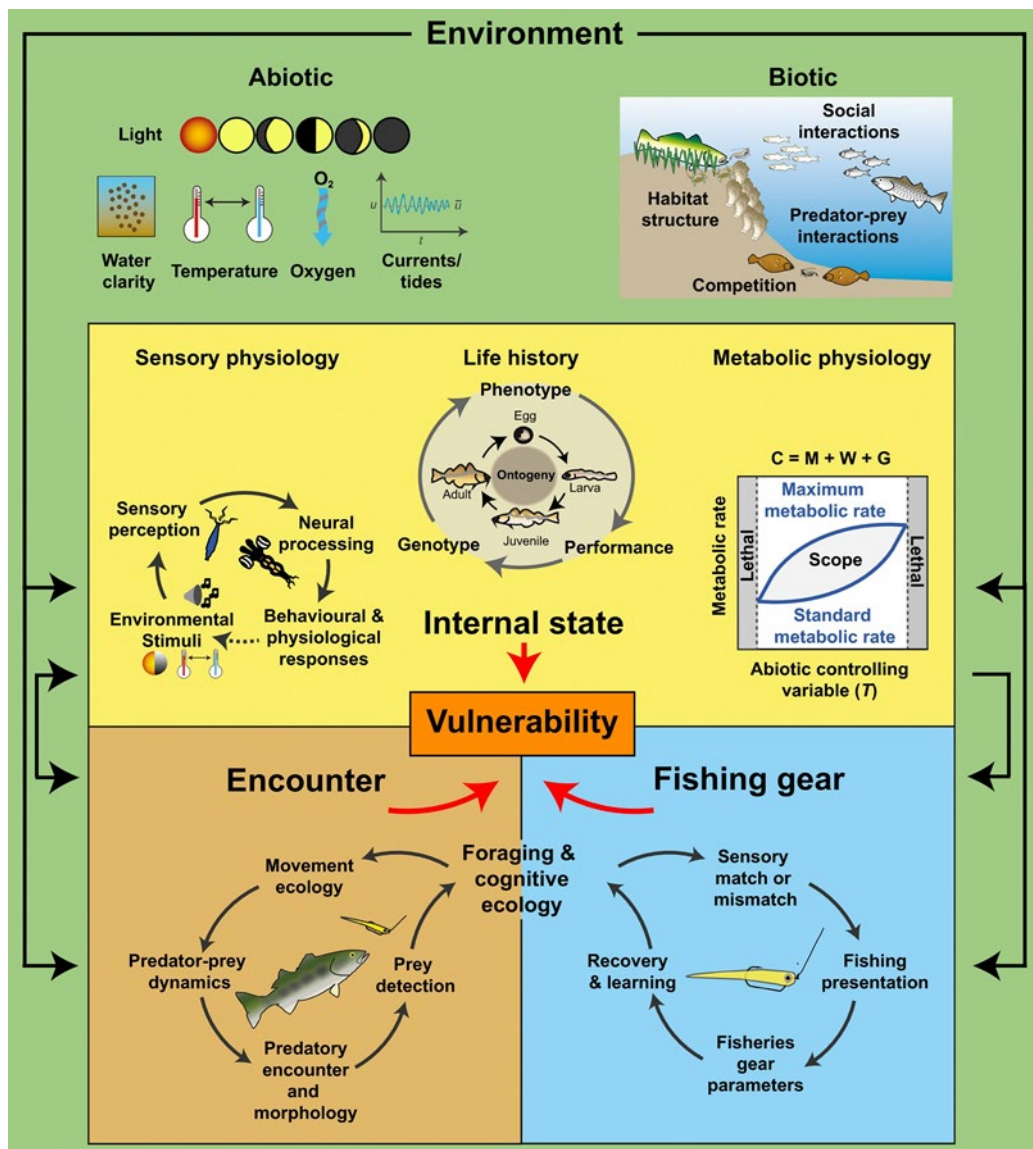
displayed larger latency times to bite at rocky habitats). Finally, *S. scriba* arriving short time after the camera deployment showed shorter latency time to bite. Conversely, no effects of exposure to fishing or *S. scriba* abundance were detected. These results support the relevance of the social interactions and the environmental specificities in shaping vulnerability. The role of the internal state of the fish should be considered too, as the arrival time could be a surrogate of the short-term bioenergetics state of a fish. Nevertheless, the correlational approach implemented here is only a first step towards a mechanistic understanding of the complex, interrelated processes shaping fish vulnerability to angling.

Introduction

Recreational fishing is one of the most extended leisure activities in marine coastal waters worldwide and involves a large numbers of participants (Hyder et al., 2018; Pita et al., 2018; Radford et al., 2018). Therefore, there is a growing concern about the potential effects of recreational fishing on fishery resources (Arlinghaus et al., 2019; Cooke and Cowx, 2006). Recreational fishers typically use passive gears: the fishing success also relies on the willingness of the fish to eat or attack the lure or bait (Lennox et al., 2017; Lokkeborg et al., 2005). Therefore, catches and fishing mortality depend not only on fishing effort and on fish abundance but also on fish vulnerability (i.e., the probability of being captured). However, vulnerability is a very complex variable (Figure IV—1; reproduced from Lennox et al., 2017) resulting from a number of interrelated processes that has been clustered into three main categories: (1) processes related with the internal state of the individual (e.g., hunger); (2) processes affecting the encounter

probability with the fishing gear (e.g., fish movement); and (3) processes related with the gear itself (e.g., size-dependent selectivity). Moreover, all the processes involved can be modulated by several environmental (biotic and abiotic) factors (Lennox et al., 2017).

Figure IV—1. *Factors and processes affecting vulnerability (reproduced from Lennox et al., 2017)*



The conceptual frame proposed by Lennox et al. (2017) suggests also to consider that vulnerability as a dynamic state variable of each fish (e.g., it can change within the same fish, between individuals of the same species, between sites, along the ontogeny,...). The processes that may affect vulnerability are diverse and they may be interrelated in complex ways (Figure IV—1). One example is that fish from marine reserves are more vulnerable to passive gears and fish vulnerability decreases when increasing the distance to marine reserves (Alós et al., 2015). Possible explanations of such a pattern may be the prevalence of different types of behaviour: Fish from heavily exploited sites seems to display shyer, less aggressive behaviour than fish from marine reserves where fishing is banned. However, the underlying process of this pattern remains elusive. For example, behavioural differences may be related with either learning (Askey et al., 2006; Lovén Wallerius et al., 2020) or selective mortality against bolder behavioural phenotypes (Alós et al., 2016; Monk et al., 2021). Moreover, provided that marine reserves may display enhanced abundances of some species, denso-dependent processes (i.e., inter- or intra-specific competition) may lead to a reduced per-capita food availability, which in turn drives to some bioenergetics deficit, that is known to enhances foraging movement (Campos-Candela et al., 2019b), which finally increases vulnerability (Alós et al., 2012). Thus, cause-effects chains are expected to be complex.

Irrespective of the complexity of the processes behind, the ecosystem and community level interactions are expected to play a relevant role in shaping vulnerability (Ward et al., 2006). For example, different predator landscapes, differences in shelter densities or its interaction may depict contrasted fear landscapes, which may modulate vulnerability. Moreover, social interactions may buffer (or trigger) behavioural responses leading to vulnerability changes. For example, exploitative competition can make the bait

unavailable to the less efficient feeders (i.e., gear saturation); whereas some individuals may actively prevent the access to the baits by others fish (interference competition). The attack rate could also be enhanced by the presence of perceived competitors (social facilitation). Moreover, habitat-specific differences in vulnerability have been reported too (Lennox et al., 2017; Stoner, 2004). These differences may be related not only with the biotic components of the ecosystem (for example, some of the social interactions mentioned above) but also with temperature, light, turbidity, wind, currents, tides and other abiotic variables that may directly affect the detectability or the accessibility of the gear, or affect indirectly the willingness of the fish to attack the gear (Stoner, 2004).

A relevant outcome of the existence of spatio-temporal variations in vulnerability is that fish abundance may be decoupled with catches, which leads to hyperdepletion (catch rate declines more quickly than fish abundance; Hilborn and Walters, 1992) or hyperstability (more skilled anglers overrides any behaviourally-based decoupling of the catch rate and fish abundance; Ward et al., 2013). Although decoupling between catch rate and abundance seems more common than it was previously believed, the processes behind remains unknown too (Alós et al., 2015). Therefore, a better understanding of the processes affecting vulnerability, and the outcomes of vulnerability in the resource dynamics are essential for assessing the potential effects of recreational fishing on fishery resources. Field measurements on vulnerability of wild fish have been made possible after the extensive use of baited remote underwater video (BRUV; Alós et al., 2015; Díaz-Gil et al., 2017). Here we use BRUVs for measuring a surrogate of vulnerability (latency time to bite, or the time a fish lasts to attack the bait) and exploring the correlational patterns of such a latency to bite with a number of potential explanatory variables. The case study focuses in *Serranus scriba*, an abundant, benthic, small-sized, carnivorous species that is

one of the main targets of the recreational fishers at the Balearic Islands (Alós and Arlinghaus, 2013; Dedeu et al., 2019). We specifically assessed the effects on vulnerability-to-angling of variables related with social interactions (e.g., number and behaviour of other conspecific fish and fish of other species) and environmental characteristics (e.g., habitat type, depth, season or exposure to fishing).

Materials and Methods

Overview

Provided that the objective is to relate the response variable (latency to bite, or the time spent by a given fish to attack the bait) with a number of potential explanatory variables, the statistical unit of the analysis is the time period between a given fish appear in the scene until it, eventually, attacks the bait or disappear. This time is equivalent to the full, continuous track of a given fish in a video scene. Accordingly, potential explanatory variables must be measured at this scale. However, some variables can be assumed to be constant at larger spatio-temporal scales. Thus, several scales have been actually considered: (1) variables summarizing events during the latency to bite (e.g., average number of fish counted in the scene during the latency to bite), (2) variables summarizing events along the full deployment time (e.g., the maximum number of fish counted at any frame in a full video), (3) variables specific of the camera deployment location (e.g., depth or sea bottom characteristics), (4) site-specific variables (absolute abundance of *S. scriba*; see 0) and (5) season-specific variables (e.g., late spring vs late summer comparison).

The explanatory variables recorded and the *a priori* expected process(es) that depict each one of those variables are summarized at Table IV-1.

Table IV-1. Overview of the explanatory variables considered.

Variable	Scale	Source/Observations	Processes
Habitat	Habitat score 1 Habitat score 2 squared Habitat score 1 squared Habitat score 2	Camera deployment location	The habitat scores result from a multivariate analysis on the cover percentages of sand, seagrass and rocks recorded at the camera deployment location.
Depth		Camera deployment location	Food availability (long-term bioenergetics). Fear landscape. Shelter availability. Community level interactions (predators, competitors). Denso-dependent processes. Differences in the dynamic of the olfactory cues.
Time since sunset		Camera deployment time	Food availability (long-term bioenergetics). Fear landscape. Shelter availability. Community level interactions (predators, competitors). Denso-dependent processes.
Arrival time		Latency to bite of a given <i>S. scriba</i>	Short-term bioenergetics. Circadian rhythm. Light-related, anti-predator behaviour.
S1: number of fish of any species biting the bait		Latency to bite of a given <i>S. scriba</i>	Short-term bioenergetics.
S2: number of fish of any species not biting but clearly interested by the bait		Latency to bite of a given <i>S. scriba</i>	Social interactions (Community level).
S3: number of fish of any species near the bait but not clearly interested on it		Latency to bite of a given <i>S. scriba</i>	Social interactions (Community level). Inter-specific competition. Gear saturation. Interference competition. Social facilitation.
Diversity of the species attracted by the bait		Camera deployment time	Social interactions (Community level). Inter-specific competition. Gear saturation. Interference competition. Social facilitation.
Nmax-like		Camera deployment time	Social interactions (Community level).
Number of <i>S. scriba</i> biting the bait (conspecific fish)		Latency to bite of a given <i>S. scriba</i>	Social interactions. Intra-specific competition. Gear saturation. Interference competition. Social facilitation.
Number of <i>S. scriba</i> around the bait.		Latency to bite of a given <i>S. scriba</i>	Social interactions. Intra-specific competition. Gear saturation. Interference competition. Social facilitation.
Absolute abundance of <i>S. scriba</i>		Site-specific variable	Social interactions. Intra-specific competition. Denso-dependent processes.
Exposure to fishing.		Camera deployment location	Differential mortality (behavioural type). Learning. Denso-dependency (released competence at heavily exploited sites). Food availability. Long-term bioenergetics.
Season		Season-specific effects (Spring vs Summer)	Denso-dependency. Population dynamics (e.g., recruitment). Food availability. Long-term bioenergetics.
Interaction between season and fishing effort		Camera deployment location	Provided that fishing effort peaks at Summer, but Summer fishing outcomes are expected to be larger at heavily exploited sites.
Site-specific random effects		Site	Differential mortality (behavioural type). Learning.
Camera deployment location-specific random effects		Camera deployment location	Random noise and any other unaccounted process at the site level.
			Random noise and any other unaccounted process at the deployment location level.

In addition, for completeness, the multivariate pattern of species turnover along the deployment time has been described. Finally, the maximum number of *S. scriba* counted at any moment during the deployment time (a Nmax-like metric) were compared with the absolute number of *S. scriba* (i.e., number of fish per area unit as estimated in 0) in order to evaluate the existence of possible biases related with the use of baited cameras when assessing fish abundance. Note that multivariate description of the fish community using the relative abundances directly obtained with the baited cameras used here has been explicitly avoided because the fish counted seems to be unrelated with fish absolute abundance (results reported and discussed below).

Study area and sampling design

The study was conducted alongside the South coast of Mallorca, Western Mediterranean Sea (Figure IV—3), between May 7th and August 2nd 2018, and covered 15 sampling sites (Figure IV—3, Table IV-2). Five sites were located at protected areas with different regulations (*El Toro*, *Sa Dragonera*, *Cap Enderrocat*, *Sa Conillera* and *Cabrera*) and ten sites were fully open to recreational fishers (*Cala Egos*, *Es Molinar*, *Portal Vells*, *S'Arenal*, *Cap Blanc*, *Cala en Tugores*, *Cala Pi*, *Camp de Mar*, *Badia Blava* and *S'Estanyol*). A full description of the sites is provided in Chapter III (see also Follana-Berná et al. 2021). Each site was sampled twice, at late Spring and late Summer. A total of 138 underwater camera devices were deployed in those 15 sites (Table IV-2). All the sites included large areas of suitable habitat for *S. scriba* (0), including different combinations of rocks, seagrass and sand (Fasola et al., 1997). Deployment locations within each site were randomly selected with a minimum distance of 250 m between them in the same Season to avoid between cameras interference. BRUVs deployments were

conducted between 9:30 and 13:30 local time (CET). The cameras were always deployed at locations with suitable habitat for *S. scriba*, but trying to maximize between-location environmental variability. The BRUV device consisted in a stainless steel structure, with two cameras and a horizontal dipstick of 2 m length. A fake device emulating a fishing gear was attached to the end of the dipstick (Alós et al., 2015). The cameras horizontally focuses on the fake gear, which consisted in a 1.5 m monofilament nylon line (0.35 mm) with four baited but dysfunctional hooks (size 4; gape 7.30 ± 0.03 mm). The fake gear was attached to the end of the dipstick and a floater in the opposite end keeps it upwards all the time. The bait was a piece of shrimp (*Penaeus vannamei*), which is the most common bait used by the local anglers (Alós, 2009; Morales-Nin et al., 2005). The bait was bound with Lycra® for preventing that it could be detached from the hook. Baits were replaced after every deployment. Each BRUV was deployed on the sea floor during a maximum of 30 minutes at each deployment location (Figure IV—2).

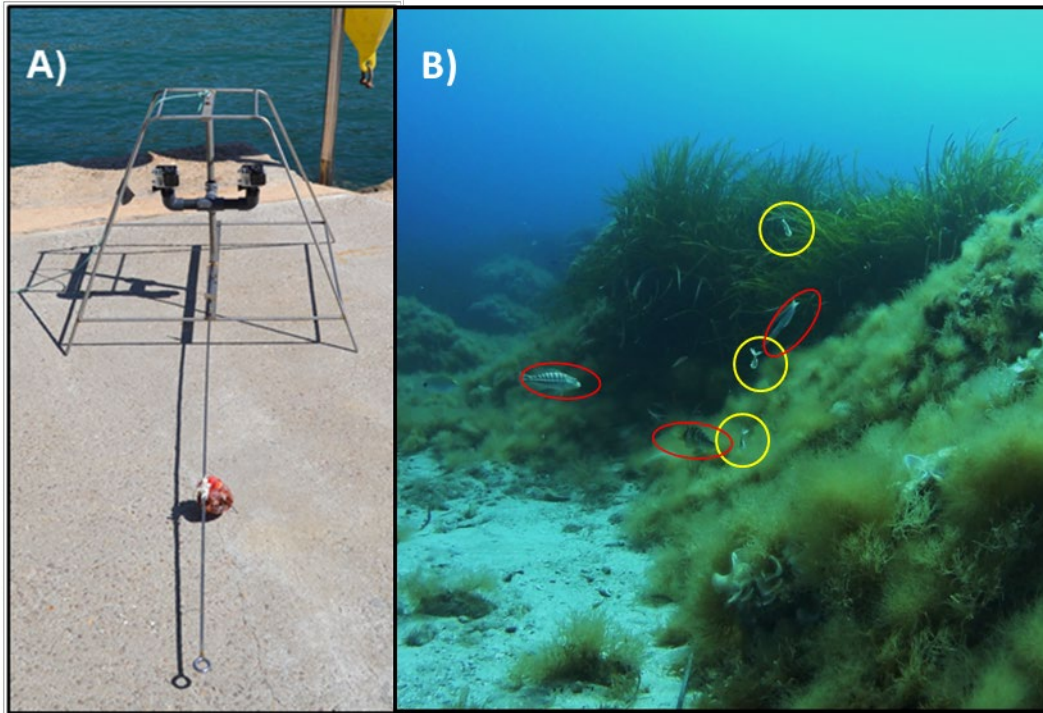


Figure IV—2. (A) BRUV device using in the field. (B) Image representing a common situation during the visualitation of the BRUV videos. The red circles are the target fishes and the yellow circles are the bait used.

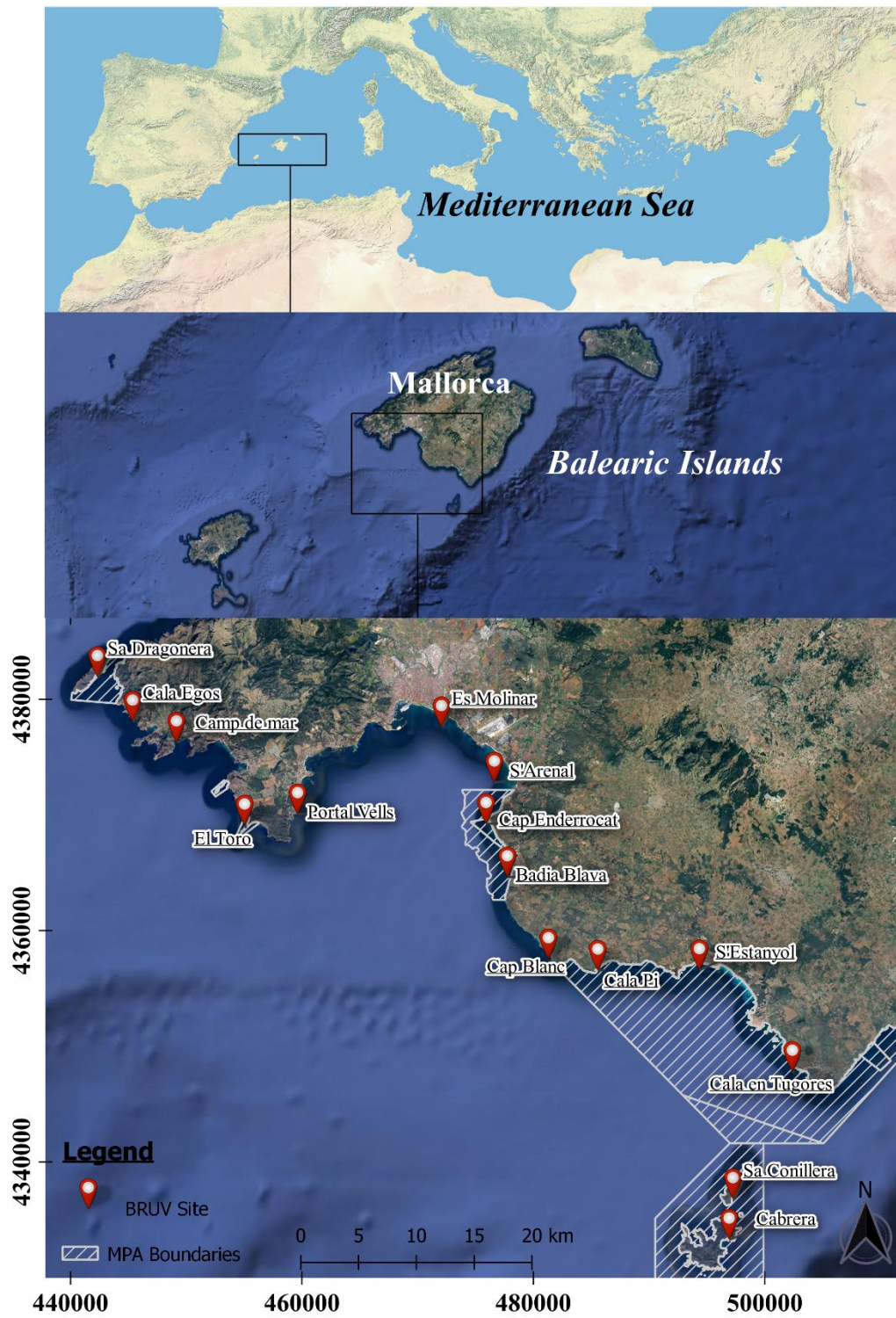


Figure IV—3. Map with the sampling sites along the south western coast of Mallorca

Table IV-2. *Sampling sites characteristics: Number of cameras deployed in each season and the total (Season 1, Season 2 and Total), diversity (Margalef's index) and total number of observed species in each site (N° Species).*

Site	Season 1	Season 2	Total
<i>S'Arenal</i>	5	5	10
<i>Badia Blava</i>	6	5	11
<i>Cap Blanc</i>	5	5	10
<i>Cabrera</i>	6	0	6
<i>Cala Pi</i>	5	6	11
<i>Camp de mar</i>	5	5	10
<i>Sa Conillera</i>	6	0	6
<i>Sa Dragonera</i>	5	5	10
<i>Cala Egos</i>	5	5	10
<i>S'Estanyol</i>	5	6	11
<i>Es Molinar</i>	5	0	5
<i>Portal Vells</i>	3	7	10
<i>Cap Enderrocat</i>	6	5	11
<i>El Toro</i>	7	0	7
<i>Cala en Tugores</i>	5	5	10
Total	79	59	138

Video reading: all fish species

The protocol for extracting social information (between-fish interactions) related with any fish species consisted in recording data at minimum 15 slots, the 95% where between 15 and 18, the maximum number of slot from a video was 33. A slot consisted in a 10 seconds scene of the video and they were placed one minute apart each other

(Figure IV—4). This procedure minimizes the processing time while maximizing the detectability of any slow-moving fish, which otherwise may remain undetected when inspecting a single frame only. Preliminary trials were completed for ensuring that this protocol ensures proper species identification and proper characterization of fish behaviour. The first minute just after the BRUV deployment was excluded from any further analyses to allow the bait to take effect and to avoid any disturbance related with BRUV deployment itself.

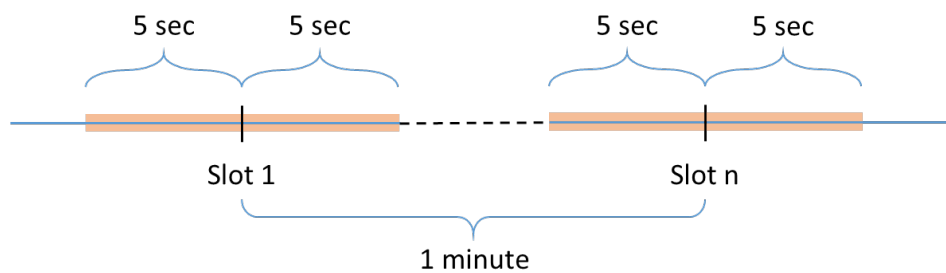


Figure IV—4. Schematic representation of selected temporal slots from each video recorded sampling.

All fish were counted and identified to the species level at each of these 15 slots. Moreover, the behaviour of any fish was classified into four categories: (1) Category *Biting*: the fish tries to swallow the bait; (2) Category *Interested*: the fish is close to the bait and shows clear interest for it. This behavioural category also includes staring the bait, swimming in circles around the bait or swimming towards the bait; (3) Category *Uninterested*: the fish swims near the bait but does not show clear interest for it; and (4) Category *Background*: the fish is in the scene but far away from the bait.

Video reading: S. scriba

Each video was fully screened when extracting information regarding *S. scriba*. The moment (exact frame) when a given *S. scriba* appears in the scene, the moment(s) when it (eventually) bites the bait and the moment that it leaves the scene or the video ends were recorded. The full track from a given fish appears in the scene until the fish bites for first time (or leaves the scene) is assumed to be an independent observation. The response variable (latency to bite: *LB*, or the time between the moment a given *S. scriba* appears at the scene until it bites the bait for first time) has been measured for each track. It is assumed that this time is a surrogate of fish vulnerability (Follana-Berná et al., 2021). Accordingly, the proper statistical strategy for analysing the latency to bite is a survival analysis (i.e., a time-to-event analysis; Klein et al., 2016). When a given fish do not bite the bait, the track is considered to be a right-censored observation (i.e., we know for sure that the fish has not bitten the bait at least during the track-specific censoring time).

The social explanatory variables corresponding to a given track that considered all species (variables *S1* to *S3* in Table IV-1) were derived from the records described in the section above (*Video reading: all fish species*) after define a smoothing function (using the *splinefun* function from the R package), integrate this function (using the *integrate* function from R) between the beginning and the end of the track, and finally normalizing by the track duration. This procedure was imposed for the need of linking the slot data (count records are available at each minute only) with the continuous time records for each *S. scriba* track. The resulting metrics are equivalent to the average counts of events along the track.

The three variables intended to measure the social interactions of a given *S. scriba* with other *S. scriba* (number of *S. scriba* biting the bait during the latency to bite, number of bites of any other *S. scriba* and number of *S. scriba* present around the bait; Table IV-1) were directly derived from the continuous observational records of all the events in any given track. However, provided that the number of *S. scriba* biting the bait and the number of bites of any other *S. scriba* are highly correlated, only the second variable was included in the statistical model described below.

Other potential explanatory variables considered

The Margalef's diversity index (Margalef, 1958) was calculated for each camera deployment location according to $(S_i - 1) / \ln(N_i)$, where S_i is the number of species of the location i , and N_i is the total number of individuals in the location i . These figures were obtained after pooling all the slot-level data of a given video. Only fish with behavioural categories *Biting* and *Interested* were included.

The fish abundance at each camera deployment location was derived from the maximum number of fish (of any species) counted at any of the slots screened in a given video. This metric emulates the *maxN* index (the maximum number of individuals seen in any frame/period over a whole video; Cappelletti et al., 2004).

The sea bottom features of the specific location where a given camera device was deployed were quantified using the percentages covered by three clear-cut types of substrates (Follana-Berná et al., 2020): (1) hard substrate with low roughness (i.e., sandy to gravel bottoms); (2) hard substrate with high roughness (i.e., rocky bottoms with many crevices and sharp slope changes, with a variable cover of small-sized algae); and (3)

seagrass (*Posidonia oceanica*). The cover percentages were transformed according to $\log(X_i/\text{geo.mean}(X))$, where X_i is one of the three percentages and *geo.mean* is the geometric mean of the three percentages at a given point (Aitchison, 1983). Finally, a Principal Component Analysis was completed on the transformed percentages. The number of axis to be retained (either one or two) was defined using the *rndLambdaF* function from the *PCDimension* package (Coombes and Wang, 2019). The PCA's scores on the retained axes were used as potential explanatory variables for the latency to bite of *S. scriba*.

In order to facilitate a more intuitive interpretation of the habitat scores, the camera deployment locations were classified into discrete habitat types (March et al., 2013). The function *fviz_nbclust* from the *factoextra* library was used to estimate the optimal number of discrete categories (Kassambara and Mundt, 2020). After that, the k-means algorithm from the *kmeans* function (R Core Team, 2021) was used to assign each camera deployment location to one of the discrete habitat types.

The depth of each sampling location was extracted in-situ using the boat's deep probe. The time after sunrise, was extracted using the *getSunlightTimes* function from the *suncalc* package (Thieurmel and Elmarhraoui, 2019) from the date and hour recorded during the fieldwork.

As mentioned above, fishing effort is expected to affect vulnerability, thus the studied area is particularly well suited for evaluating this hypothesis because recreational fishing is one of the main leisure activities in the Balearic Islands (Western Mediterranean Sea) as indicated by the high number of fishing licenses issued (Gordoa et al., 2019; Grau, 2008; Morales-Nin et al., 2015, 2005). Distance to ports has been used as a proxy of

commercial fishing effort (Caddy and Carocci, 1999). Accordingly, and following the rationale developed by March, (2014), the variable *exposure to fishing* (Table 1) of a given camera deployment location was defined from a gravity model of the distance between the deployment to all the ports on the south coast of Mallorca. These least-cost distances were estimated using the *costDistance* function from the *gdistance* package (van Etten, 2017). These distances were weighted by the number of sport fishing licenses of each port (years 2014 to 2016, data provided by the *Direcció General de Pesca i Medi Mari, Govern Illes Balears*). Finally, the *exposure to fishing* index was also weighted by the scaled number of days that recreational fishing is allowed at a given site (0). That is, this additional weight is zero at no-take marine reserves, one at fully open sites, or something between at partial marine reserves, depending on the number of days per week that fishing is allowed:

$$Exposure_{fishing_i} = (\sum_{j=15} FishingLicences_j / PortDistance_{j \rightarrow i}) *$$

$$MPA's Fishing days_i \quad \text{Equation IV-1}$$

where *i* is each camera deployment location and *j* is each port.

Finally, the sampling season was also included in the model allowing for (1) two different intercepts (between season differences) and (2) two different slopes for the fishing effort at late Spring versus late Summer (i.e., an interaction term). The rationale for including this interaction term is the large fishing impact that takes place during Summer in Mallorca (Cabanellas-Reboredo et al., 2014; March, 2014). Thus, latency to bite may experience some change related with learning or selective mortality in Summer but only at the most heavily exploited sites.

Statistical model

The latency to bite (time since a given *S. scriba* appears at the scene until it bites the bait for first time) has been assumed to be exponentially distributed, which is the canonical expectation for time-to-event successes (Klein et al., 2016):

$$LB_i \sim \mathbf{dexp}(\lambda_i) \quad \mathbf{Equation IV-2}$$

where LB_i is the latency to bite of the i fish and λ_i is the inverse of the success rate. The log-transformed λ_i is modeled as a linear combination of all the variables listed above (Table IV-1), which ensures that λ_i will be strictly positive irrespective of the values of the slopes (θ_j) of the variables considered (X_j ; note that X_j was standardized by subtracting the mean and dividing by the standard deviation):

$$\lambda_i = e^{(\theta_j X_j + R_{video,i} + R_{site,i})} \quad \mathbf{Equation IV-3}$$

Two random effects were considered: the common variability attributable to all the *S. scriba* that have appeared at the same video and the common variability attributable to all the *S. scriba* from the same location (R_{video} and R_{site}). For shake of simplicity, these two random effects were assumed to be independent (non-nested). The random components of the fish i were assumed to be normally distributed with zero mean and standard deviations σ_{video} and σ_{site} .

The parameters of the model were estimated using a Bayesian approach. The posterior probability distribution for each parameter was inferred moving Monte Carlo Markov Chains (MCMC), as implemented in JAGS 4.3.0 (Plummer, 2015). The priors for all the slopes in θ_j were assumed to be normally distributed with zero mean and a huge variance. The priors for the inverse of the variances of the random effects were assumed

to be gamma distributed with scale = 0.01 and shape = 0.01. Some fish did not bite the hook during the time interval monitored. As usual in survival analyses, those LB_i values were considered right-censored in the sense that latency to bite must be larger than the observation period ($limit_i$). This fact was modeled using the *dinterval* distribution in JAGS, that generates the likelihood for $Prob(isCensored_i | y_i, limit_i)$ for the parameters LB_i (unobserved) and $limit_i$.

Posterior probability distributions were estimated from 10,000 iterations per chain, after a burn in period of 10,000 iterations, a thinning factor of 10, and three Markov chains. Convergence was then evaluated through visual examination of trace plots of MCMC chains and assessing the *R.hat* values (a statistic that compares within- and between-chain variability; Gelman and Shirley, 2011). The analysis were implemented with an ad-hoc R script (R Core Team, 2021) that used the *R2Jags* package (Su and Yajima, 2015).

The full model (i.e., the model including all the variables listed in Table IV-1) was submitted to a step-by-step backward model selection procedure. At a given step, the variable which 95% credibility includes zero were removed. When more than one variable fit this criterion, the variable that showed the largest fraction of its posterior distribution around zero were first deleted.

Describing species turnover

The existence of a linear relationship between the species composition and the (log-transformed) time since a camera has been deployed on the sea floor was explored using redundancy analysis (RDA; Borcard et al., 2018). The hypothesis tested is that

species-specific dynamics are at play when fish are attracted by the bait. The time effect on species composition was evaluated with the model:

$$sp_{i,j,k} = \log(slot_{j,k}) + Condition(camerak) \quad \text{Equation IV-4}$$

where sp_{ijk} is the number of fish counted for the species i at the slot j by the camera k , $slot_{jk}$ refers to the time slot, and *Condition* here indicates that the camera has been considered as a covariable (i.e., any camera-specific pattern has been removed prior to evaluating the effect of time).

The abundance data were the number of fish behaving accordingly to the categories *Biting* or *Interested* but only the 9 most abundant species (which represent 95% of all the fish) were included in the analysis. Counts were Hellinger-transformed (Borcard et al., 2018), thus empty slots (slots with no fish) have been excluded. Abundance was not standardized, thus the weight of a given species in shaping the multivariate space was proportional to the species' abundance. The model (Equation IV-4) was evaluated using the *rda* functions of the *vegan* library (Oksanen et al., 2018) in R.

Abundance of S. scriba: Comparing baited and unbaited cameras

Finally, the maximum number of *S. scriba* counted at any slot during the deployment time of the baited cameras used here (an *Nmax*-like metric) were compared with the absolute number of *S. scriba* (i.e., number of fish per area unit) as estimated using unbaited cameras (see 0), in order to evaluate possible biases related with the use of baited cameras for assessing fish abundance.

Results

More than 2,500 minutes (or 41 hours) of video were screened and interpreted from the 138 locations sampled at 15 different sites. Latency to bite was measured from 386 *S. scriba*.

Species detected, diversity and behavioural traits

A total of 33 different fish at specie-level were recorded and identified, with a total of 10,820 individuals counted (Table IV-4). The number of species per site ranged from 20 (*Sa Dragonera*) to 9 (*Es Molinar* and *Portals Vells*). Species diversity (Margalef's Index, as estimated using fish counts from the baited cameras) varied between 1.29 (*Portals Vells*) and 3.59 (*Sa Conillera*) (Table IV-3).

Table IV-3. *Margalef's Index and Total number of species per site.*

Site	Margalef's Index	N° Species
<i>S'Arenal</i>	2,26	16
<i>Badia Blava</i>	1,52	10
<i>Cap Blanc</i>	1,8	13
<i>Cabrera</i>	2,37	15
<i>Cala Pi</i>	1,65	13
<i>Camp de mar</i>	2,51	18
<i>Sa Conillera</i>	3,59	18
<i>Sa Dragonera</i>	2,58	20
<i>Cala Egos</i>	2,19	17
<i>S'Estanyol</i>	1,79	12
<i>Es Molinar</i>	1,4	9

<i>Portal Vells</i>	1,29	9
<i>Cap Enderrocat</i>	1,69	12
<i>El Toro</i>	2,3	15
<i>Cala en Tugores</i>	1,7	12

Nine species accumulates 95% of all the recorded fish (*Diplodus annularis*, *Coris julis*, *Chromis chromis*, *Symphodus tinca*, *Serranus scriba*, *Diplodus vulgaris*, *Symphodus mediterraneus*, *Symphodus ocellatus*, *Symphodus rostratus*) (Table IV-4). *Diplodus annularis* was the most detected species (3,105 fish), followed by *Coris julis* (3,073 fish) and *Chromis chromis* (2,084 fish). In contrast, the least detected species were *Sparus aurata* (1 fish), pelagic species such as *Thunnus thynnus* (1 fish) and *Lichia amia* (1 fish), and the Chondrichtids *Myliobatis aquila* (1 fish) and *Dasyatis pastinaca* (2 fish), all of them recorded far from the BRUVs (behavioural categories *Uninterested* and *Background*) (Table IV-4).

Table IV-4. Total number and proportion of individuals observed for each species according to recorded behavioural traits: S1: Biting; S2: Interested; S3: Uninterested; S4: Background.

Specie	Biting		Interested		Uninterested		Background		Total	Percentage	Accumulated
<i>Diplodus annularis</i>	1039	33,46%	1199	38,62%	719	23,16%	148	4,77%	3105	28,70%	28,70%
<i>Coris julis</i>	692	22,52%	1363	44,35%	684	22,26%	334	10,87%	3073	28,40%	57,10%
<i>Chromis chromis</i>	199	9,55%	706	33,88%	667	32,01%	512	24,57%	2084	19,26%	76,36%
<i>Symphodus tinca</i>	21	3,20%	351	53,42%	165	25,11%	120	18,26%	657	6,07%	82,43%
<i>Serranus scriba</i>	147	25,79%	273	47,89%	104	18,25%	46	8,07%	570	5,27%	87,70%
<i>Diplodus vulgaris</i>	42	14,09%	118	39,60%	78	26,17%	60	20,13%	298	2,75%	90,45%
<i>Symphodus mediterraneus</i>	47	18,80%	156	62,40%	40	16,00%	7	2,80%	250	2,31%	92,76%
<i>Symphodus ocellatus</i>	48	23,53%	119	58,33%	28	13,73%	9	4,41%	204	1,89%	94,65%
<i>Symphodus rostratus</i>	8	8,99%	55	61,80%	25	28,09%	1	1,12%	89	0,82%	95,47%
<i>Symphodus cinereus</i>	17	22,97%	38	51,35%	17	22,97%	2	2,70%	74	0,68%	96,16%
<i>Spondylosoma cantharus</i>	9	13,04%	43	62,32%	10	14,49%	7	10,14%	69	0,64%	96,79%

<i>Oblada melanura</i>	10	16,95%	13	22,03%	19	32,20%	17	28,81%	59	0,55%	97,34%
<i>Atherina hepsetus</i>	1	2,13%	5	10,64%	17	36,17%	24	51,06%	47	0,43%	97,77%
<i>Unknown</i>	2	6,06%	13	39,39%	8	24,24%	10	30,30%	33	0,30%	98,08%
<i>Symphodus spp.</i>	0	0,00%	0	0,00%	0	0,00%	25	100,00%	25	0,23%	98,31%
<i>Thalassoma pavo</i>	5	20,00%	8	32,00%	8	32,00%	4	16,00%	25	0,23%	98,54%
<i>Pagellus erythrinus</i>	1	4,76%	8	38,10%	11	52,38%	1	4,76%	21	0,19%	98,73%
<i>Serranus cabrilla</i>	2	9,52%	9	42,86%	7	33,33%	3	14,29%	21	0,19%	98,93%
<i>Spicara smaris</i>	1	5,56%	4	22,22%	10	55,56%	3	16,67%	18	0,17%	99,09%
<i>Diplodus sargus</i>	2	13,33%	4	26,67%	2	13,33%	7	46,67%	15	0,14%	99,23%
<i>Sarpa salpa</i>	0	0,00%	0	0,00%	0	0,00%	15	100,00%	15	0,14%	99,37%
<i>Mullus surmuletus</i>	0	0,00%	0	0,00%	12	85,71%	2	14,29%	14	0,13%	99,50%
<i>Symphodus doderleini</i>	0	0,00%	4	57,14%	3	42,86%	0	0,00%	7	0,06%	99,57%
<i>Symphodus roissali</i>	1	14,29%	4	57,14%	2	28,57%	0	0,00%	7	0,06%	99,63%
<i>Sciaena umbra</i>	0	0,00%	0	0,00%	0	0,00%	7	100,00%	7	0,06%	99,70%
<i>Gobius spp.</i>	5	71,43%	2	28,57%	0	0,00%	0	0,00%	7	0,06%	99,76%
<i>Labrus merula</i>	0	0,00%	3	50,00%	2	33,33%	1	16,67%	6	0,06%	99,82%
<i>Symphodus melanocercus</i>	0	0,00%	3	50,00%	2	33,33%	1	16,67%	6	0,06%	99,87%
<i>Spicara maena</i>	0	0,00%	0	0,00%	5	100,00%	0	0,00%	5	0,05%	99,92%
<i>Sphyaena sphyraena</i>	0	0,00%	0	0,00%	0	0,00%	3	100,00%	3	0,03%	99,94%
<i>Dasyatis pastinaca</i>	0	0,00%	0	0,00%	2	100,00%	0	0,00%	2	0,02%	99,96%
<i>Thunnus thynnus</i>	0	0,00%	0	0,00%	0	0,00%	1	100,00%	1	0,01%	99,97%
<i>Sparus aurata</i>	0	0,00%	0	0,00%	0	0,00%	1	100,00%	1	0,01%	99,98%
<i>Myliobatis aquila</i>	0	0,00%	0	0,00%	0	0,00%	1	100,00%	1	0,01%	99,99%
<i>Lichia amia</i>	0	0,00%	0	0,00%	0	0,00%	1	100,00%	1	0,01%	100,00%
Total	2299	21,25%	4501	41,60%	2647	24,46%	1373	12,69%	10820		

Regarding behavioural traits (Table IV-4), 62.8% of the fish detected was observed either biting (behavioural category *Biting*, 21.2%) or showing interest towards the bait (behavioural category *Interested*, 41.6%). The records assigned to the behavioural categories *Uninterested* or *Background* were 24.5% and 12.7% respectively. In the case of the key specie, *S. scriba* the 25.8% of the fish sampled bite the bait, the 47.9% showed interest for the bait and were close to it, the 18.2% not were interested and the 8.1% were far for the bait in the background.

Environmental variables

In spite that the cameras were deployed at sites well within the suitable habitat for *S. scriba*, we have been successful in selecting locations along a wide environmental gradient, thus the sampling design is fully appropriate for detecting any potential correlational pattern between latency to bite and the environmental variables considered. Concerning the habitat, almost all cameras have been deployed at locations showing some cover of seagrass (*P. oceanica*). However, the gradient of habitat specificities was wide. The pattern of between-location similarity regarding the habitat features is shown at Figure IV—5. The two axes retained from the PCA on the cover percentages explained all (100%) the observed variance. The variance explained by each of these two axis was similar (56.4% and 43.6%). According with the scores on these two axes, the camera deployment locations have been classified into six discrete categories for facilitating an intuitive interpretation of the habitat characteristics. The six habitat categories are: 1) sandy bottoms (Sand), 2) seagrass meadows with some rock patches (Seagrass with Rock), 3) full seagrass meadows (Seagrass), 4) mixed habitats with seagrass, sand and rocks (Mix), 5) rocky bottoms (Rock), and 6) seagrass meadows with some sandy patches (Seagrass with Sand) (Figure IV—5).

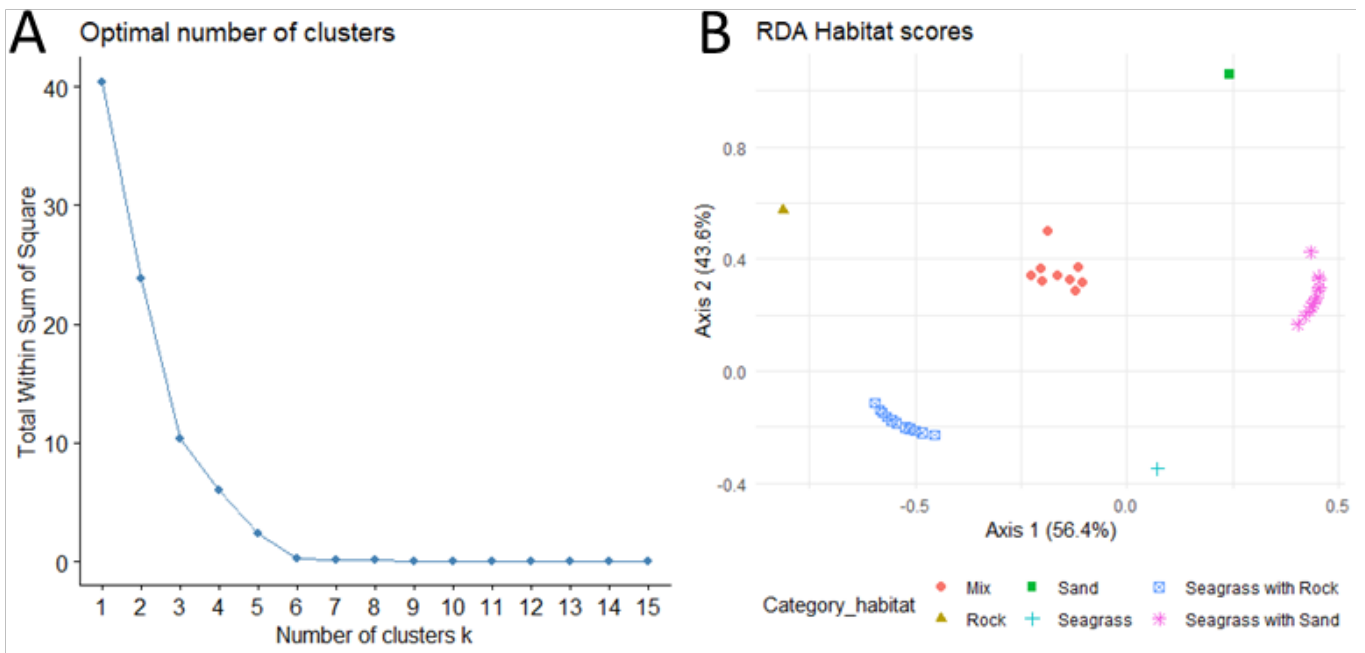


Figure IV—5. *A) Optimal number of cluster (habitats). B) Site scores on the first two RDA axis on the Aitchison-transformed percentage cover.*

The depth of the camera deployment locations ranged from 3 m to 26 m, corresponding these two extreme values to cameras deployed in *Sa Dragonera*. The average depth of all the cameras deployed was 13.3 m. The range sampled covers the depth range inhabited by *S. scriba* (Fasola et al., 1997). The time elapsed from sunrise until cameras deployment ranged between 2 hours and 27 minutes and 7 hours and 27 minutes, with an average of 4 hours and 32 minutes after sunrise. Concerning the *exposure to fishing* index, the range of the sites sampled covered from no-take marine reserves (e.g., *Cabrera*) to heavily exploited sites that are close to many of the ports at Palma Bay (e.g., *Es Molinar*).

Vulnerability of *S. scriba*

The model resulting after step-by-step backwards model selection (intermediate steps from the full, initial model to the final model are detailed in the repository <https://doi.org/10.17632/t573gvfg9.1> (Follana, G. & Palmer, M., 2021) was composed by only five variables: (1) the habitat score #1, (2) the arrival time (time since the camera deployment), (3) the number of fish from any species that are already biting the bait, (4) the number of fish from any species that show *Uninterested* behaviour for the bait and (5) the number of *S. scriba* present around the bait (Figure IV—6 and Table IV-5).

Table IV-5. *Estimated slope values of the five variables applied in the model selection (see Figure IV—6). SD: Standard deviation, BCI: Bayesian credibility interval. R.hat: potential scale reduction factor, which explains how the chains have converged to the equilibrium distribution. Approximate convergence is diagnosed when the upper limit is close to 1.*

Variable	Mean	SD	BCI 2.5%	Median	BCI 97.5%	R.hat
slope Habitat score 1	0,365	0,137	0,101	0,36	0,639	1
slope Arrival time	-0,621	0,116	-0,86	-0,616	-0,405	1,01
slope S1: number of fish of any species biting the bait	0,309	0,093	0,119	0,311	0,493	1
slope S3: number of fish of any species near the bait but not clearly interested on it.	-0,369	0,121	-0,602	-0,37	-0,142	1
slope Number of <i>S. scriba</i> around the bait.	0,391	0,052	0,271	0,397	0,478	1
Intercept	-8,227	0,232	-8,702	-8,216	-7,799	1,02

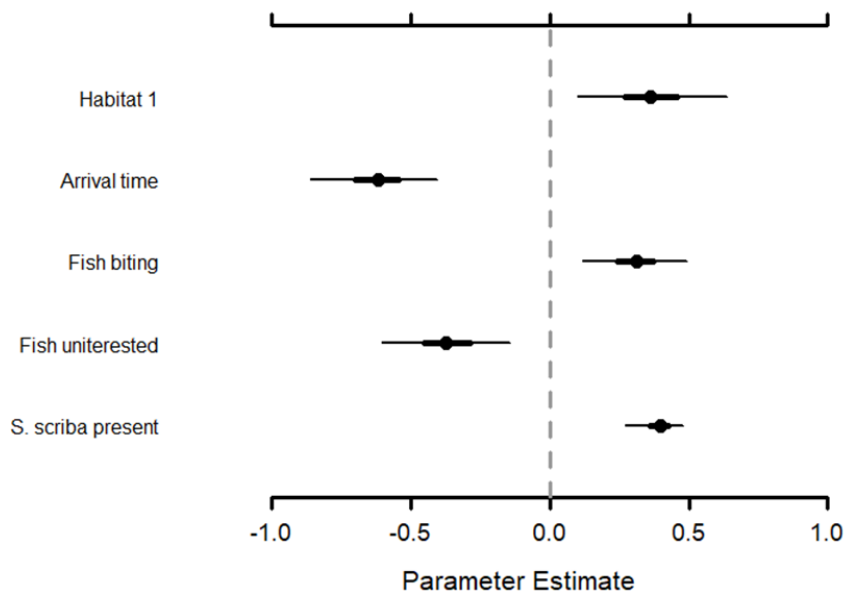


Figure IV—6. Model effects. The lines shows the median and the spread of the confidence interval (94% and 75% CIs) for the slopes of the five retained variables.

The median latency to bite of *S. scriba* (i.e., the expected time at a hypothetical site displaying the average values for all the five variables retained) was estimated in 1.7 minutes but 95% bootstrap-inferred interval ranges from 3.8 seconds to 10.2 minutes. The expected effects of each variable were assessed by bootstrapping: In turn, a given variable was allowed to vary along the actually observed gradient while the other variables were kept constant at their average value. Concerning the arrival time, the fish arriving to the bait after a short time from the cameras deployment tend to have shorter latency to bite (i.e., they are more vulnerable). When a large number of fish of any species are already biting the bite, the latency to bite of *S. scriba* tend to be shorter (i.e., they are more vulnerable). *S. scriba* seems to display shorter latency to bite at rocky habitats (i.e., they are more vulnerable). When other *S. scriba* are already surrounding the bait, the latency

to bite of a new *S. scriba* tend to decrease (i.e., they are more vulnerable). Finally, when a large number of fish are swimming around the bait but do not show any interest toward it, *S. scriba* tend to display larger latency to bite (i.e., they are less vulnerable) (Figure IV—7). The processes that may drive these patterns are discussed below.

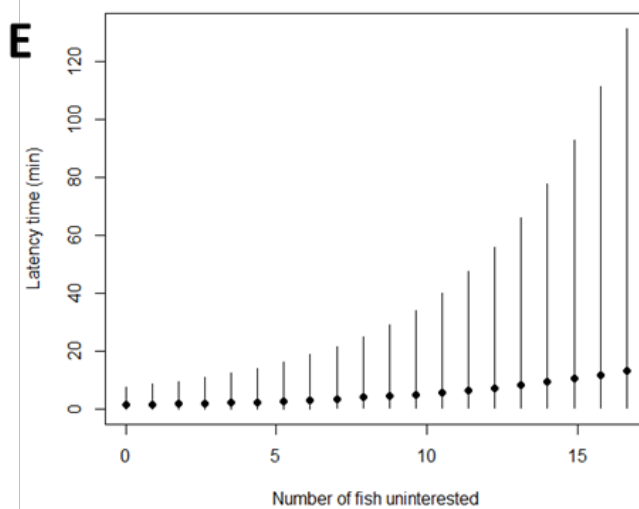
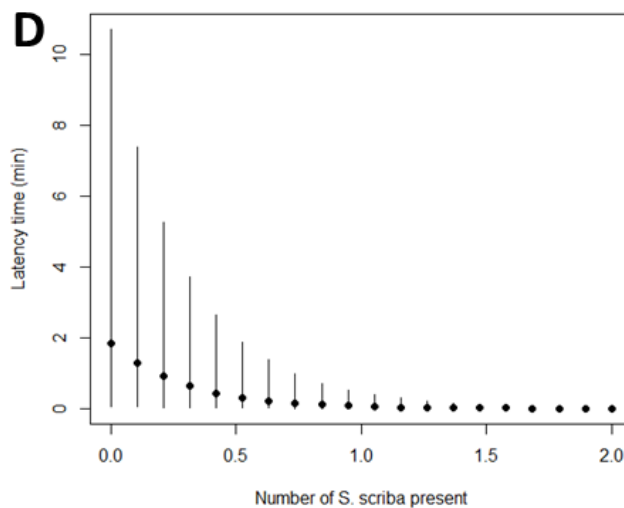
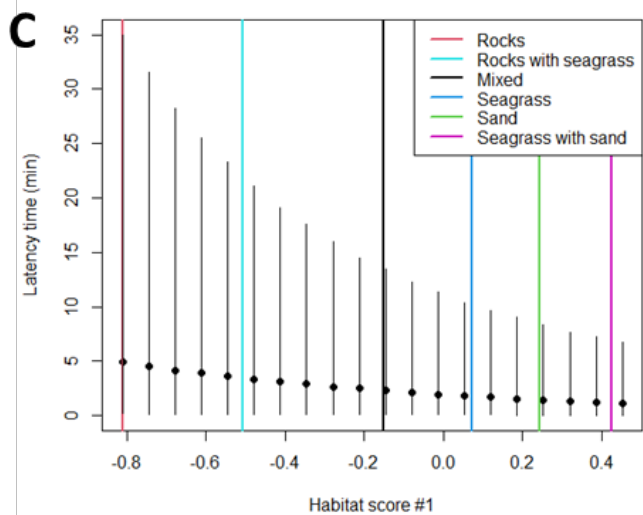
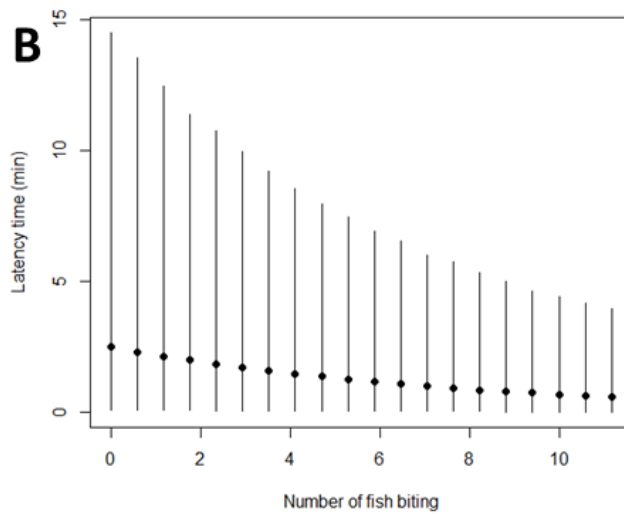
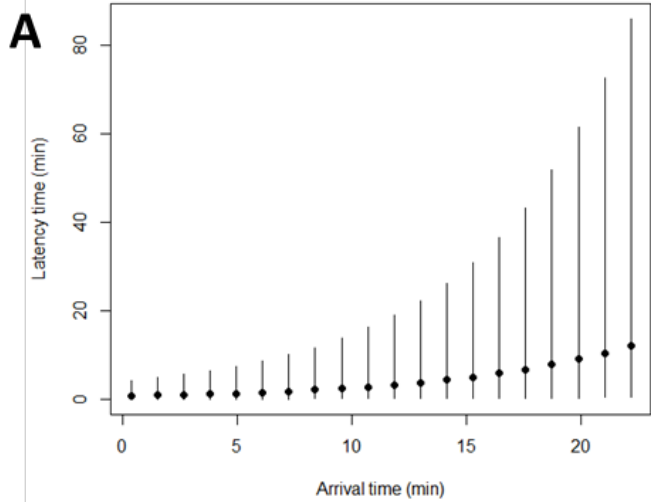


Figure IV—7. Description of relevant effects (95% BCI does not include zero) on Latency to bite the bait for *Serranus scriba*. The dot is the average value of the expected patterns and the vertical lines the SD for A) Arrival time, B) Number of fish biting, C) Habitat score 1, D) Number of *S. scriba* presents and E) Number the fish uninterested. The Y-axis shows the time in minutes.

Among the variables for which no relevant effect on latency to bite have been detected, it should be highlighted the case of *exposure to fishing*. Neither this variable nor its interaction with season (late spring versus late summer) seem to have any effect on the latency to bite of *S. scriba*.

Species turnover

In spite that some fish of most of the species remains around the bait for 15 or more minutes, each species seems to appear in the scene at its own species-specific moment (Figure IV—8). Similarly, each species tends to remain more or less time around the bait. For example, *Coris julis* peaks around 3 minutes after the camera deployment, while the bulk of *Diplodus annularis* seems to reach the bait later, around 6 minutes after the camera deployment. The species scores better depict the species turnover after the multivariate analysis (RDA) of the number of fish counted by species and slot (Figure IV—9). Concerning the nine most detected species, the arrival rank to the bait was (1) *Coris julis*, (2) *Serranus scriba*, (3) *Symphodus tinca*, (4) *Diplodus annularis*, (5) *Symphodus rostratus*, (6) *Symphodus ocellatus*, (7) *Diplodus vulgaris*, (8) *Chromis chromis*, (9) *Symphodus mediterraneus*.

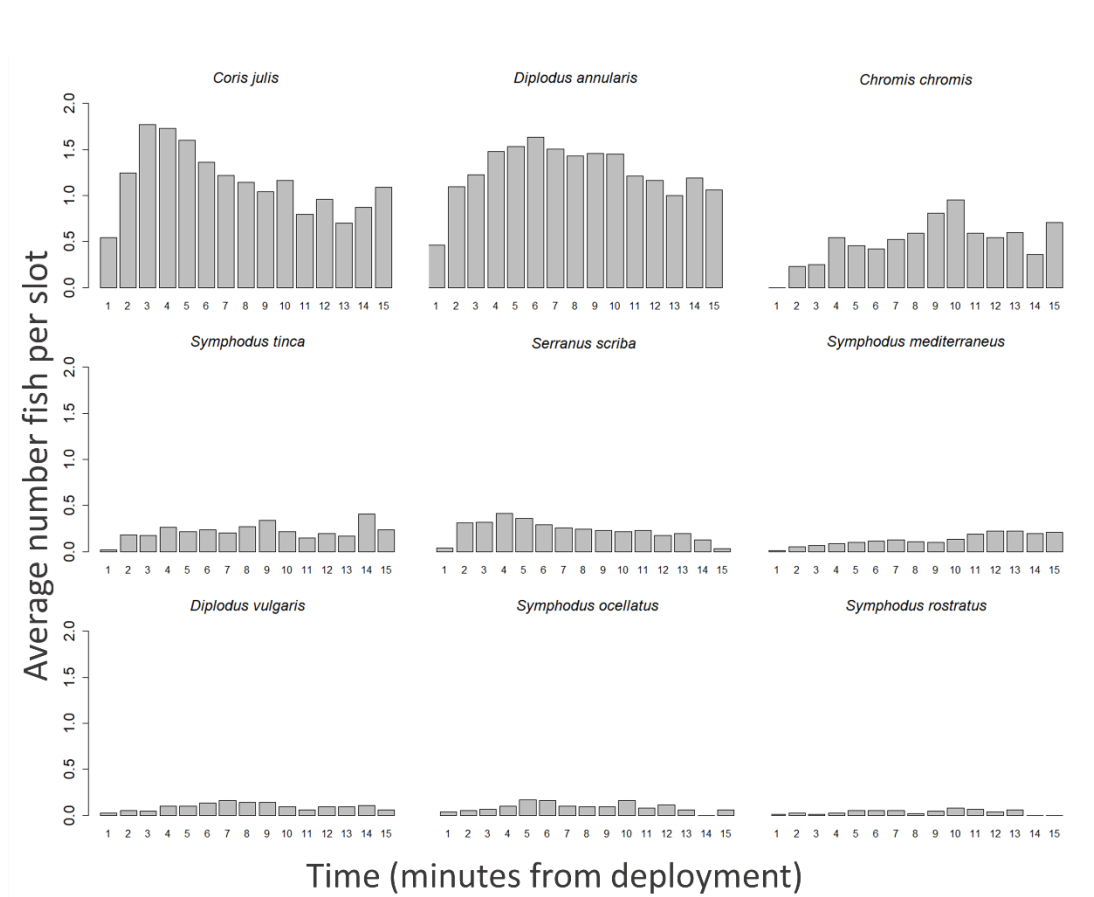


Figure IV—8. Temporal pattern of the nine most abundant species (representing the 95% of the fish). The x-axis represents the time after the camera deployment (15 slots). The y-axis represent the averaged (across cameras) number of fish displaying either behavioural category Biting or Interested.

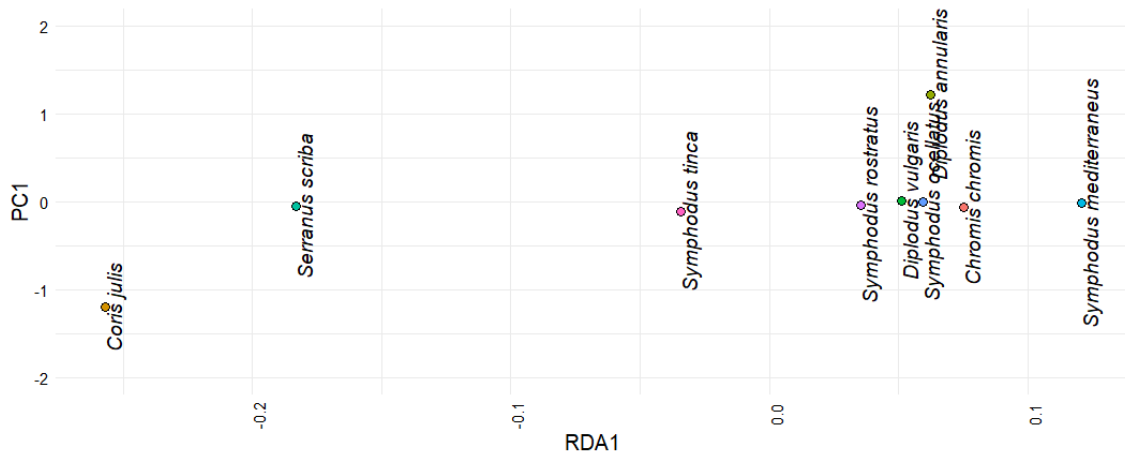


Figure IV—9. RDA plot showing the order of appearance of each species (species turnover).

Comparing baited and unbaited cameras for assessing *S. scriba* abundance.

The maximum number of fish detected in any frame of a video has been proposed to be a reliable proxy for relative abundance. This metric, known as *maxN* (Cappo et al., 2004; Ellis and DeMartini, 1995; Rhodes et al., 2020), has been also applied to the maximum number of fish detected in video slots (Díaz-Gil et al., 2017). Thus, the maximum number of *S. scriba* in any of the slots screened here can be used for deriving a *maxN*-like index for each location where a camera device has been deployed. Moreover, absolute abundance estimates (fish/km²) are available for the same sites but using unbaited cameras (0). The later method has been demonstrated to render unbiased estimates of fish density (Abolaffio et al., 2019; Campos-Candela et al., 2018; Campos-Candela et al., 2019a; Follana-Berná et al., 2020, 2019), thus they constitute a ground truth standard against which the *maxN*-like index can be compared. The values obtained using both methods are shown in Figure IV—10.

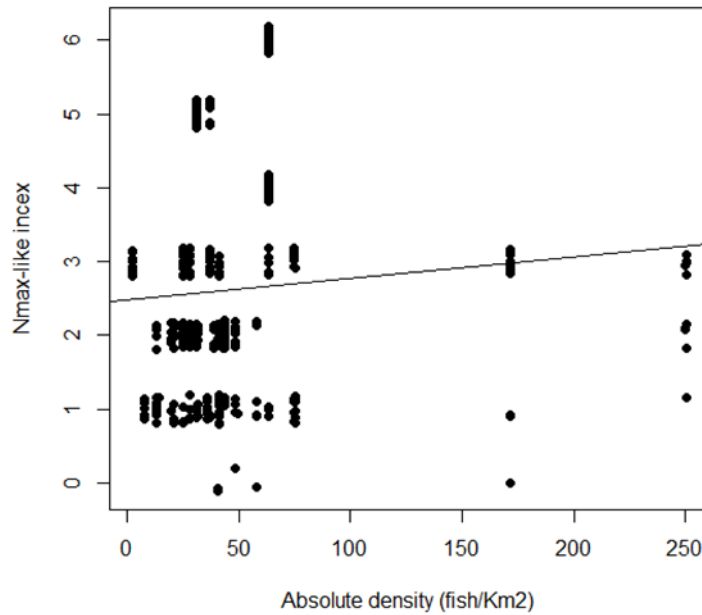


Figure IV—10. Comparison of the estimates of absolute density (fish/Km²) obtained with unbaited cameras (0) against the maximum number of *S. scriba* counted at any slot of a video obtained with a baited camera. The points have been slightly moved to better show the all the cameras deployment sites.

The maxN-like index was clearly uncorrelated with the absolute abundance of *S. scriba* (Pearson correlation $r = 0.09$). It is particularly noteworthy that sites as *Cabrera* that display absolute abundance values more than 100 times larger than sites as *Es Molinar*, showed the same or very close number of fish when attending the relative abundance values obtained using baited cameras (3 fish). The results at the site level are qualitatively the same.

Discussion

Most of the species targeted by the recreational fishers in Mallorca (Morales-Nin et al., 2005) has been detected by the BRUVs deployed here. After sampling 15 sites, deploying 138 camera devices and screening more than 40 hours of video, more than 10,000 fish belonging to 33 different fishes at specie-level were recorded. Most of the fish (60%) displayed behaviours included into the categories *Biting* or *Interested*, thus, these fish were potentially vulnerable to angling. Accordingly, with the sampling design, most of species recorded are benthic and linked to *P. oceanica* seagrass habitats with variable mixtures of rocky and sandy bottoms. However, a few fish from other habitat types has been detected too. Some remarkable examples are the Bluefin Tuna (*T. thynnus*), the European Barracuda (*S. sphyraena*) and large Chondrichthyes such as *Dasyatis pastinaca* and *Myliobatis aquila*. Very similar lists of species have been reported from the same biogeographical region when using baited cameras (Alós et al., 2015; Stobart et al., 2007).

The species relative abundance gathered using baited cameras has been used for describing the fish assemblages from a given site (Clarke et al., 2019; Whitmarsh et al., 2017) or to disentangle the environmental drivers that shapes species composition (Aguzzi et al., 2015). Baited cameras have been also used for assessing fish communities targeted by recreational fisheries (Lowry et al., 2012a; Willis and Babcock, 2000) or monitoring marine protected areas (Willis et al., 2000; Willis and Babcock, 2000). In the latter case, it has been suggested that the behavioural specificities displayed by the fish inhabiting MPAs may be a potential caveat when using UVC (Willis et al., 2000). Here we clearly demonstrated that the use of baited cameras introduces severe biases when

estimating the abundance of *S. scriba*, thus these problems may exceed the specific case of MPAs. Certainly, the use of baited cameras is, at first glance, more appealing because a huge number of fish can be identified in comparison with the small numbers recorded when using unbaited cameras. Nevertheless, the results reported here clearly discourage the blind use of baited cameras for assessing the abundance of a given species (Cheal et al., 2021; Colton and Swearer, 2010; Lowry et al., 2012b; Sheaves et al., 2020).

These drawbacks apply to the community level too. For example, the detection of emblematic species as tunas, barracudas or large Chondrichthyes is exciting but anecdotic. Moreover, the dynamics of the response to the attraction cue generated by the bait seems to be species-specific. One of the outcomes is the clear species turnover reported above. However, it is plausible that the use of other baits (Ghazilou et al., 2016; Wraith et al., 2013) or under different environmental scenarios the species turnover may change (Schmid et al., 2017). In our case, the number of detected individuals of *C. julis* peaks only 3 minutes after deploying a camera, thus this species might be acting as a visual flag for a social facilitated behaviour in other species. This flag role has been described for *C. julis* at the within-species level: some individuals display conspicuous foraging movements while others remain sheltered until a prey is detected (Kruschel and Schultz, 2012). Therefore, depending on the actual species assemblage of a given site and on a poorly known but probably complex web of environmental and social effects, the image of the species composition and/or species diversity obtained with baited cameras is expected to be uncertain. Again, the use of baited camera for assessing abundance is appealing but its extensive use requires an in depth understanding of the attraction dynamics and the processes involved.

However, it should be noted that the attraction dynamics is one of the essential processes shaping vulnerability (Figure IV—1). Therefore, the use of baited cameras as those we have developed here is fully justified when the objective is identifying the main correlational patterns affecting latency to bite (as a surrogate of vulnerability). Here we have demonstrated that latency to bite in *S. scriba* is correlated with five variables. Three of them (number of fish already biting, number of other *S. scriba* in the scene and number of fish displaying *uninterested* behaviour) are clearly related with social interactions. In two cases (number of fish already biting and number of other *S. scriba* in the scene), an increasing number of fish/events is correlated with shorter latency to bite, thus larger vulnerability to angling. The processes behind these patterns remains elusive due to the correlational nature of the sampling design. However, it could be speculated that inter- or intra-specific competition and/or social facilitation may play a role, which is supported by empirical evidences: fish increases the feeding rate when they perceive increasing levels of interference competition (Dill and Fraser, 1984). The third social variable correlated with latency to bite suggest the opposite pattern: when the number of fish swimming around the bait (but not directly interested by is increasing, the latency to bite of *S. scriba* increases too, thus fish becomes less vulnerable. Again, the cause-effect remains elusive but it could be speculated that the presence of a large number of non-foraging fish may trigger anti-predator, precautionary behaviour in *S. scriba*.

The fourth variable correlated with latency to bite is the arrival time. The fish arriving to the bait just after the cameras deployment tend to show shorter latency to bite (thus, they are more vulnerable) than the fish arriving later. We suggest that this pattern may be related with the short-term bioenergetics status of the fish (e.g., hunger level). It has been proposed that fish with energetic deficit tend to display enhanced foraging

behaviour, explore progressively larger areas and overcome the fear landscape imposed by a given predator setting (Campos-Candela et al., 2019b). Thus, energy-depleted fish may move more actively and may have larger chance of finding the bait (or a hook; Alós et al., 2012).

Regarding the habitat type, *S. scriba* is less vulnerable at rocky bottoms rather than at seagrass or sandier bottoms. The structural complexity and roughness are known to affect the ability of fish to locate their preys and feed (Rilov et al., 2007; Stoner, 2004). Ryer et al., (2004) reported that Pacific halibut tend to reduce foraging movement in complex habitats, thus in spite of the huge differences between this species and *S. scriba*, this is an example of habitat-dependent behaviour that may affect vulnerability in the same direction that the behaviour displayed by *S. scriba*. Nevertheless, the habitat-related vulnerability may be a direct or indirect outcome of many other processes: differences in food availability (which may drive to long-term bioenergetics differences) (Ward et al., 2006), specific fear landscape, shelter availability, several community level interactions (e.g., different settings of predators or competitors) (Connell, 1983), denso-dependent processes or even differences in the bait plume hydrodynamics (Stoner, 2004).

We did not detect relevant effects on latency to bite for none of the remaining variables, but some of them deserves special attention. We expected that fish at heavily exposed sites will display low vulnerability because this pattern has been reported for the same species and area (Alós et al., 2015). Similarly, the interaction between exposure to fishing and season was expected to be relevant. Provided that fishing effort peaks at summer in Mallorca, and that individuals fished are not a random sample but they display the most vulnerable phenotypes, either learning (Lovén Wallerius et al., 2020) or selective

mortality (Monk et al., 2021) should increase the relative number of low vulnerable fish. Finally, absolute abundance of *S. scriba* seems uncorrelated with vulnerability, in spite that any density-dependent process should lead to some bioenergetics deficit in the less competitive fish, which should become more vulnerable. We attribute these results to the correlational nature of the experimental design. When a large number of interrelated processes are underway (Figure IV—1), the cause-and-effect chain may mask some otherwise apparent effect. For example, the effect of exposure to fishing may be masked by the fact that fish at heavily exposed sites are already shyer, move less actively and, thus, enlarge the arrival time to the bait, which is the relevant effect we have actually detected. On the contrary, on those protected areas, the latency to bite of bolder fish can be directly influenced, as it was shown above, by locally higher species richness compared to areas more exposed to fishing.

Therefore, the correlational approach developed here should be just considered a first step toward a mechanistic understanding of the processes shaping vulnerability. The results reported here may help to design controlled lab experiments or exploit the use of bio-loggers (Aspillaga et al., 2021; Brownscombe et al., 2019; Rutz and Hays, 2009) for disentangling the ultimate causes of vulnerability. This mechanistic understanding of the vulnerability drivers is unavoidable when trying to forecast the effects of recreational fishing and other fisheries using passive gears, where fishing mortality and catch rate pivot on three pillars: fishing effort, fish abundance and fish vulnerability.

Acknowledgements

GFB were supported by a PhD fellowship (FPI-INIA) from the National Institute for Agricultural and Food Research and Technology (INIA). PAL was supported by a Juan de la Cierva Incorporación postdoctoral grant (IJCI-2015-25595). This work was funded by R+D project PHENOFISH (CTM2015-69126-C2-1-R; MINECO) and is a contribution of the Joint Research Unit IMEDEA-LIMIA. This study was carried out with permission from the fisheries local administration (Direcció General de Pesca i Medi Ambient del Govern de les Illes Balears). We specially thank the researchers and students involved in the fieldwork. All the authors declare that they have no conflict of interest.

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Chapter V - Consequences of trait-selective fisheries on population reproductive potential: an experimental approach.

Reference

Follana-Berná, G., Palmer, M., Campos-Candela, A., Alós, J., Ospina-Alvarez, A., Grau, A., Lowerre-Barbieri, S., Arechavala-Lopez, P., 2021. Consequences of trait-selective fisheries on population reproductive potential: An experimental approach. *Fish. Res.* 239, 105939. doi:10.1016/j.fishres.2021.105939

General Discussion

Gathering information on the biological biodiversity and abundance of marine species and is essential for effective management of marine ecosystems. Fortunately, the methods for collecting this information are quickly advancing too. This thesis highlights how the technological developments in the field of underwater cameras and their application in fish monitoring constitutes a great progress for fish conservation and fisheries management. The increase of the spatial and temporal scales along where marine observations are now available have been never seen. The safety improvement for the observers has been greatly improved too. In addition, the wealth of information that underwater cameras can collect while they remain deployed for long periods give us a broader image of what is happening under the sea, allowing to assess not only the biodiversity and abundance of fish populations, but also to understand the underlying ecological processes, to evaluate the environmental effects and to explain the behavioural interactions between species, which altogether will help to evaluate and improve the existing management plans.

Fishing-dependent sampling methods are biased and may be invasive for the ecosystem. Furthermore, many marine populations are declining and with the increasing development of MPA networks, monitoring with extractive methods are restricted or banned in many cases. Therefore, non-destructive, remote and fishing-independent sampling methods, such as those using underwater cameras, are becoming increasingly widespread for monitoring marine biodiversity. Moreover, the use of underwater cameras implies negligible risk for the observers when compared with, for example, the censuses performed by scuba divers (underwater visual censuses, or UVCs).

This thesis also highlights that there is not one fit-for-all underwater camera method, but different strategies should be the most appropriate for achieving different purposes and for dealing with different scenarios. For example, unbaited cameras, or RUVs, have been identified as an effective methodology to provide information on the absolute abundance of fish. Any progress in this technique will therefore be particularly beneficial to the management of areas with high fishing pressure or conservation interest. One of the first milestones achieved in this thesis has been the use of computer simulation experiments for estimating the sampling effort needed to obtain a precise and accurate estimate of fish density. The theoretical advances in modelling fish movement (Campos-Candela et al., 2018) has been paramount for that. Based on this approach, a new framework was developed in Chapter I. It combines UVC and RUV for the concurrent estimation of fish density (individuals per unit area) and the detection probability, or detectability (P_{ID}). Once P_{ID} is estimated, fish density can be estimated accurately and precisely at the scale of the preferred reference method using only RUV. Thus, provided that none of the commonly used reference methods for estimating density of resident coastal fish is precise enough, the possibility of an extensive use of properly calibrated RUVs may contribute to substantially enlarge the spatio-temporal scope of density monitoring programs for many resident coastal fish species.

Moreover, detectability of the same individual may depend on many variables. For example, differences in the complexity of the bottom structure may result in habitat-dependent differences in detection probability. I have explored this topic in Chapter II, where I propose the use of vertical RUVs due to some key advantages when compared to the RUVs with horizontal field view. First, when using horizontal RUVs, some fish may remain hidden by rocks or other benthic structures, and therefore remain undetected

(Zarco-Perello and Enríquez, 2019). Second, the area actually surveyed by horizontal cameras is not easily measurable and any uncertainty in this variable will be inevitably translated to fish density uncertainty. Certainly, this challenge can be solved using stereoscopic cameras, which allow the user to estimate the distance between any fish and the camera (Díaz-Gil et al., 2017), but it could involve an additional effort when analysing the videos, and may introduce a size-dependent bias (i.e., larger fish would be more detectable at larger distance from the camera). Using vertical RUVs, I demonstrated that detectability is independent of fish abundance and habitat type, at least for the case of *S. scriba* and within the environmental gradient that has been sampled. At the same time, site-specific differences in abundance has been successfully detected. However, there are some other factors influencing fish detectability that must be taken into account in future samplings. Some examples are, namely, density-dependent behaviour (Andersen et al., 2017), seasonal differences in fish behaviour (i.e., fish may be more active and thus be more easily detected in warmer seasons), physiological status of the fish (e.g., hunger, diseases, etc.), fish size, social interactions or any other species-specific behaviour. Therefore, it is mandatory to take into account the behavioural attributes of the target species prior to selecting a specific UVC and/or RUV design (Cheal and Thompson, 1997; Samoily and Carlos, 2000; Ward-Paige et al., 2010).

Once the influence of the habitat on fish detectability was assessed for vertical RUVs, an on-site assessment was carried out in Chapter III to demonstrate the feasibility and applicability of this method for monitoring coastal fish populations. Vertical unbaited RUVs were successfully used to estimate absolute densities of coastal fish populations along a coastline of more than 100 km, covering from MPAs to unprotected areas and along the entire habitat gradient inhabited by *S. scriba*. The result obtained support that

the areas with greater exposure to fishing are also those that have a lower fish density. The results reported in Chapter III suggest that fish monitoring with vertical unbaited RUVs at large spatial and temporal scales is already a reliable alternative. Moreover, in the near future, the combination of underwater cameras and artificial intelligence will represent a unique opportunity for a qualitative leap in how marine wildlife is observed. Different tools are already exploiting deep learning with similar purposes (Alós et al., 2020; Cheng et al., 2020; Connolly et al., 2021; Tabak et al., 2019; Xu et al., 2019).

The use of baited cameras has also its own target usefulness. Previous studies have shown that baited cameras (BRUVs) can be used for studying fish vulnerability to angling, which is a very relevant topic for fishery managers because catches depend not only on fishing effort and fish abundance, but also on fish vulnerability (Alós et al., 2015a; Lennox et al., 2017). Previous studies on fish vulnerability have mainly focused on the characteristics of fish (e.g., fish size) or on the environmental setting (e.g., water turbidity) but less attention has been paid on the influence of social interactions (i.e., fish-fish interactions). Therefore, in Chapter IV, BRUVs were used to better understand how the environmental conditions and the inter- and intra-specific social interactions might influence vulnerability-to-angling of *S. scriba*. I have used a BRUV device emulating the most common hook-and-line gear utilized by the recreational fishers in Mallorca. This method has first allowed describing a clear species turnover: some species are quickly attracted to the bait (e.g., *C. julis*) and they seem to trigger the visual attraction of other species (e.g., *S. scriba*). Moreover, vulnerability-to-angling is not only correlated with the number of individuals of other species interacting with the bait, but also with the number of conspecifics. In addition, the habitat characteristics and the time since the bait deployment are affecting the vulnerability-to-angling of *S. scriba* too. These findings

highlight the importance of a mechanistic understanding of the complex processes shaping vulnerability when designing management plans for the coastal fish exploited by recreational fishing.

Nevertheless, it is expected that any behaviourally selective fishing will enhance the survival probability of low vulnerable phenotypes and, thus, will increase the ratio of shy fish in the population (Alós et al., 2015a, 2015b). Accordingly, non-vulnerable individuals might act as offspring reservoirs in fish populations under artificial selection, as in the case of angling. When vulnerability is heritable, the outcome would be an evolutionary response. Therefore, fish behaviour is expected to play a key role in determining and modulating the impact of fishing on wild populations (Pine et al., 2009). In Chapter V, the relationship between vulnerability and reproductive potential of *S. scriba* was experimentally assessed. Although vulnerability-to-angling was not related neither with the total number of eggs produced nor with the seasonal spawning pattern of *S. scriba* in captivity, egg yolk size was larger in the less vulnerable fish but only towards the end of the reproductive season. Egg yolk size can be considered as a proxy for viability and egg quality (Reading et al., 2018), and therefore, some effects of vulnerability-to-angling could be suggested, although other processes should be considered when drawing conclusions related to fish spawning success. Therefore, Chapter V highlights the need for further research to improve our understanding of potential evolutionary changes in larval survival and development, as well as other changes in the life-history traits of *S. scriba* related with recreational fishing.

In summary, this thesis shows that unbaited cameras (RUVs) are highly recommended as a tool for monitoring fish populations and evaluating the success of

management plans. The application of RUVs, along with other methodologies, can exponentially increase the scientific knowledge of the dynamics of fish population, and expand the temporal and spatial range of sampling in the natural environment with an outstanding precision and accuracy. However, the process of extracting useful information from the videos should be improved. Nevertheless, given the astonishing development of new technologies, this bottleneck could be overcome within a short term. For example, the recent advances in the field of deep learning for automatic data mining can minimize the time and effort currently needed for video visualization.

In addition, this thesis demonstrates that there is not a single fit-for-all underwater camera method, and each strategy can be adapted according to the goals to be achieved. In this context, I demonstrated how BRUVs cameras could be used to better-understand the effects of recreational fisheries at both individual and population levels, but also to assess the influence of environmental and social interactions on vulnerability-to-angling. Understanding the dynamic of fish populations and the effects of recreational fisheries at different levels and perspectives is essential to improve existing management plans or to develop new ones.

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Conclusions

1. A new framework combining UVC and RUV has been developed and successfully applied to estimate fish density (individuals per area unit) and individual detectability (P_{ID}).
2. After estimating Probability of Individual Detection, absolute fish density can be estimated accurately and precisely using RUVs only.
3. In the case of *S. scriba*, fish detectability when using vertical Remote Underwater Videos is independent of the bottom-type.
4. After knowing the environmental dependencies and the species-specificities of P_{ID} , vertical RUVs can be used to monitor the abundance of many resident coastal fish, and at spatial and temporal scales relevant for taking management decisions.
5. The technological advances in underwater cameras, together with the development of artificial intelligence, represent a unique opportunity for a qualitative leap in the way marine wildlife is observed.
6. Baited cameras (BRUVs) are the appropriate tool for understanding fish vulnerability-to-angling, which should be taken into account when assessing the fishing effects.
7. The variables correlated with vulnerability in the case of *S. scriba* are social, internal and environmental.
8. Fish vulnerability to fishing are related neither with the total number of eggs produced nor with the seasonal spawning pattern of *S. scriba* in captivity.

However, vulnerability is related with egg equality. Low-vulnerable fish present higher egg-yolk size (which is expected to improve larval development and survival) toward the end of the spawning season.

Annexes

A. Supplementary material Chapter I:

Estimating the density of resident coastal fish using underwater cameras: accounting for individual detectability.

Reference

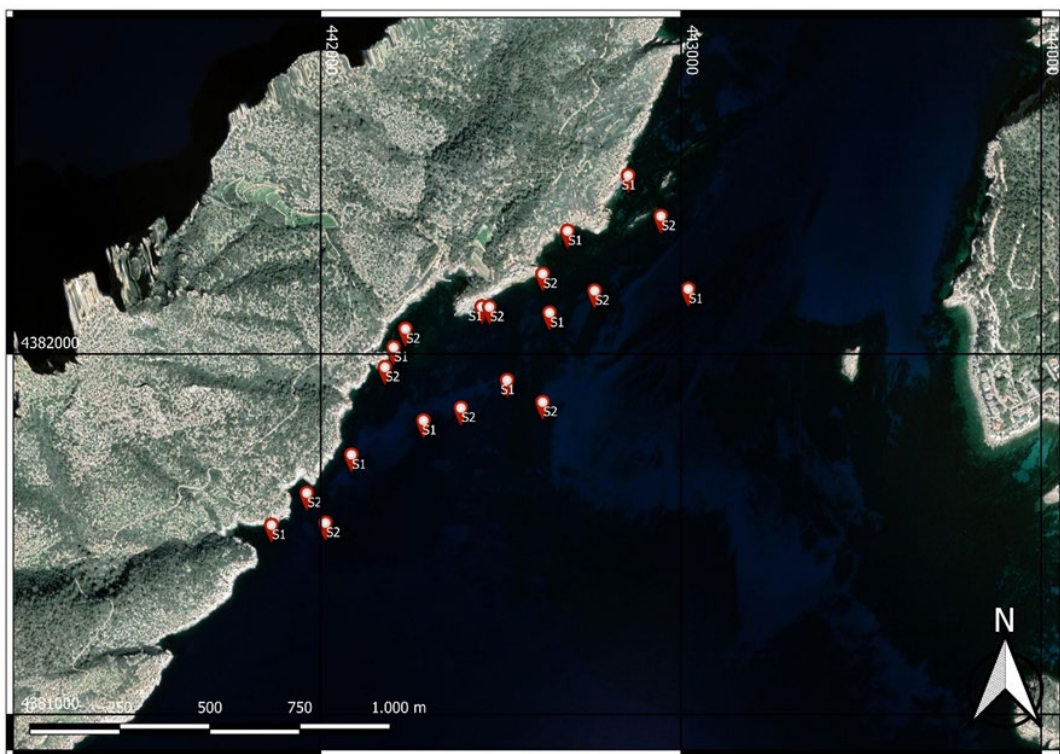
Follana-Berná, G., Palmer, M., Campos-Candela, A., Arechavala-Lopez, P., Diaz-Gil, C., Alós, J., Catalan, I., Balle, S., Coll, J., Morey, G., Verger, F., Grau, A., 2019. Estimating the density of resident coastal fish using underwater cameras: accounting for individual detectability. *Mar. Ecol. Prog. Ser.* 615, 177–188. doi:10.3354/meps12926

B. Supplementary material Chapter III:

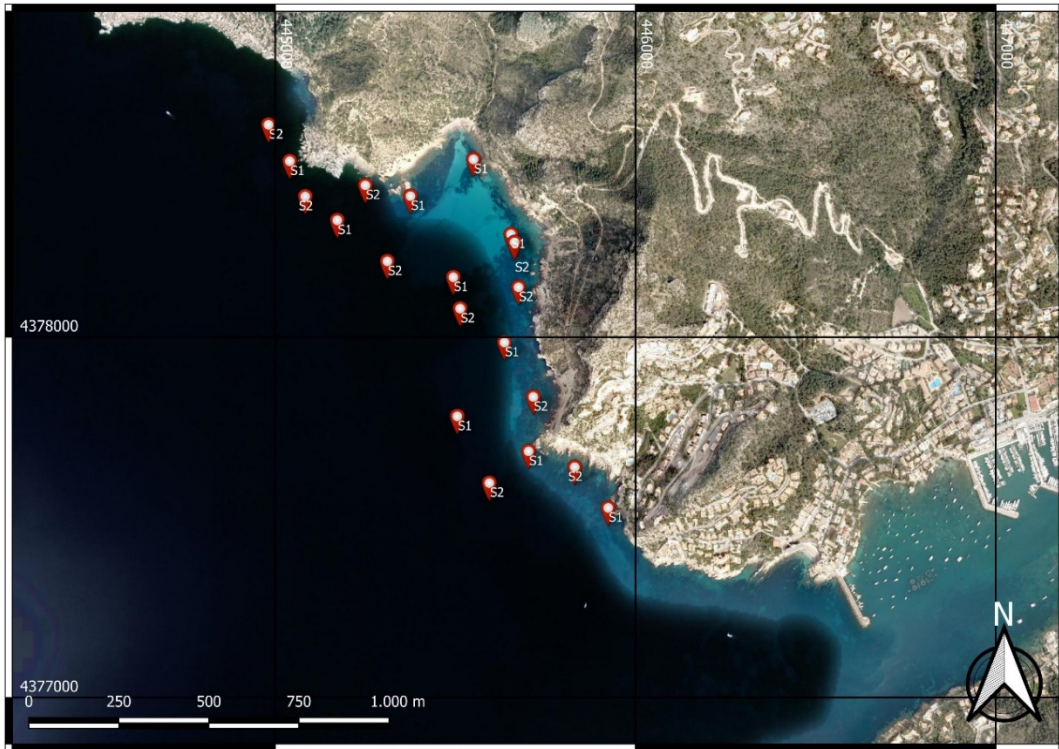
Mesoscale assessment of sedentary coastal fish density using vertical underwater cameras.

Supplementary figure B-1. *Images of all the places sampled with the points where the cameras were anchored. A) Sa Dragonera, B) Cala Egos, C) Camp de Mar, D) El Toro, E) Portal Vells, F) Es Molinar, G) S'Arenal, H) Cap Enderrocat, I) Badia Blava, J) Cap Blanc, K) Cala Pi, L) S'Estanyol, M)Cala en Tugores, N) Sa Conillera and O) Cabrera. S1, Spring. S2, Summer.*

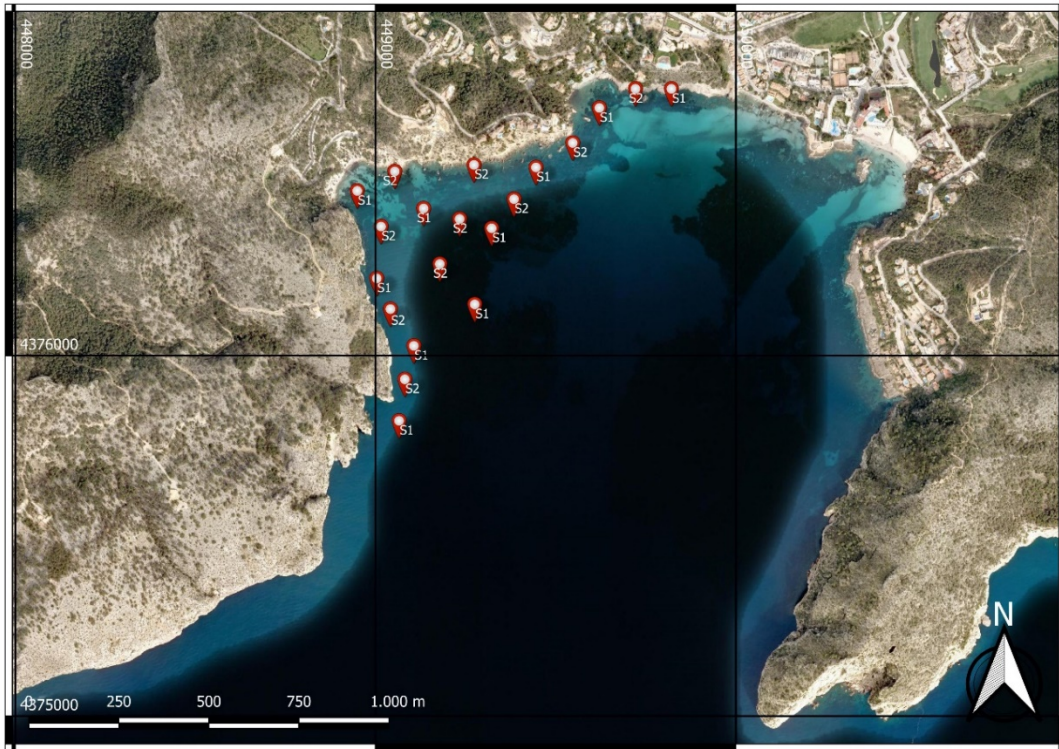
A)



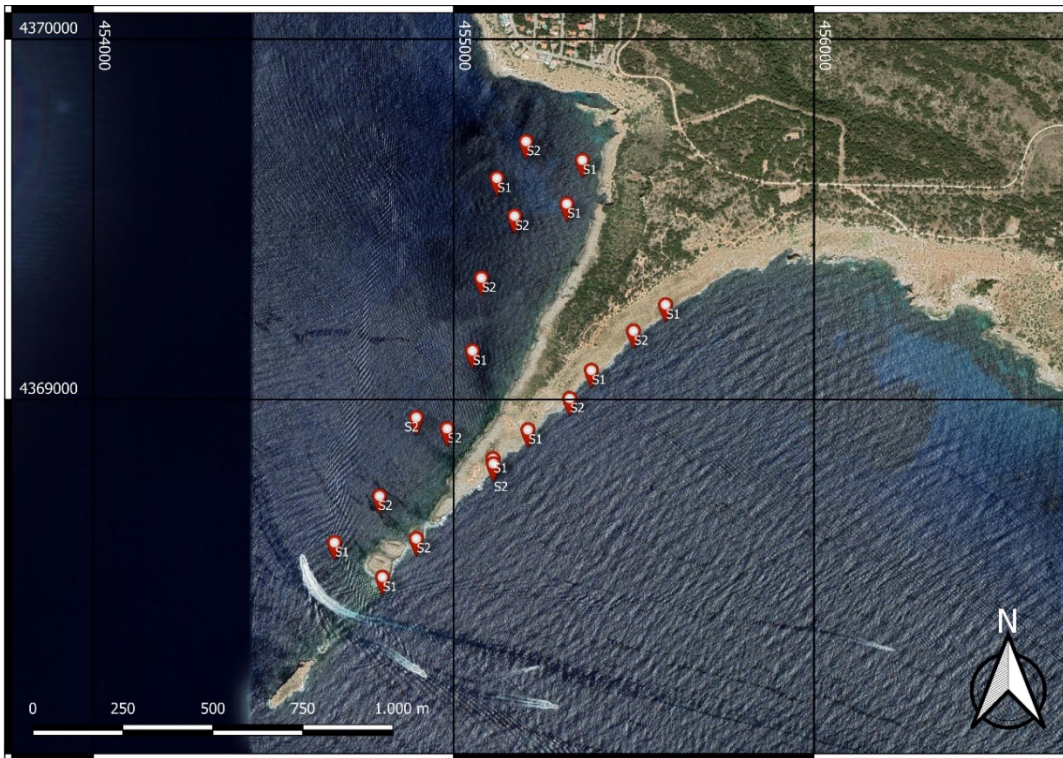
B)



C)



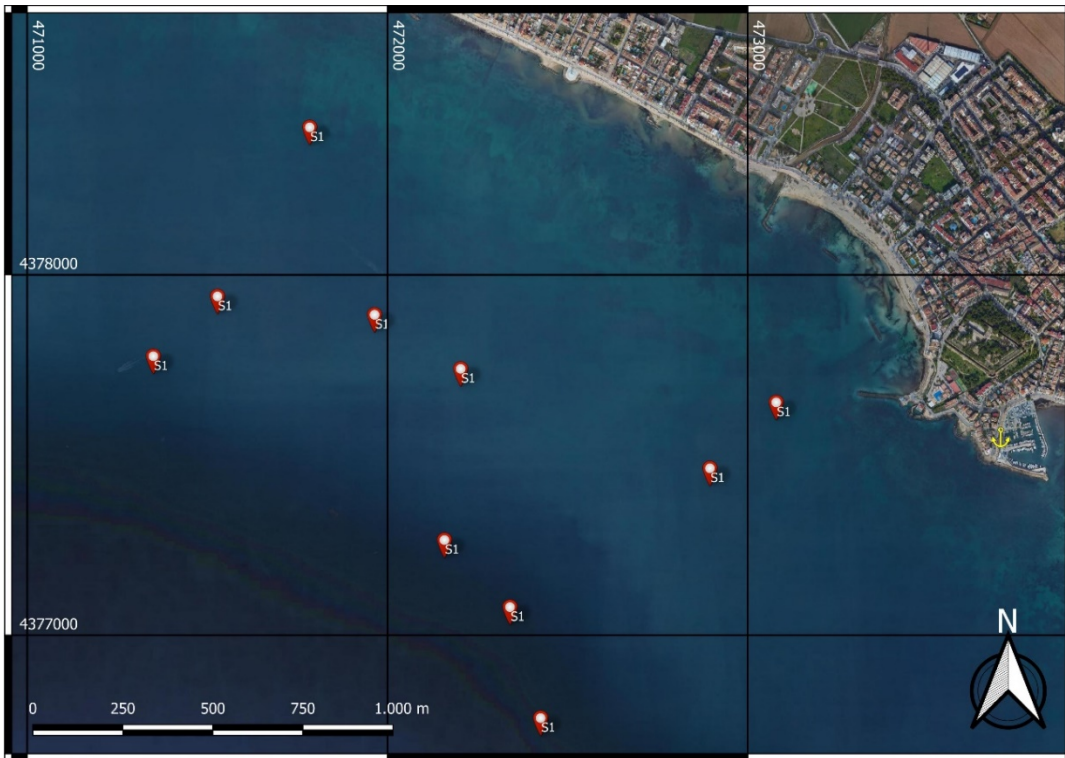
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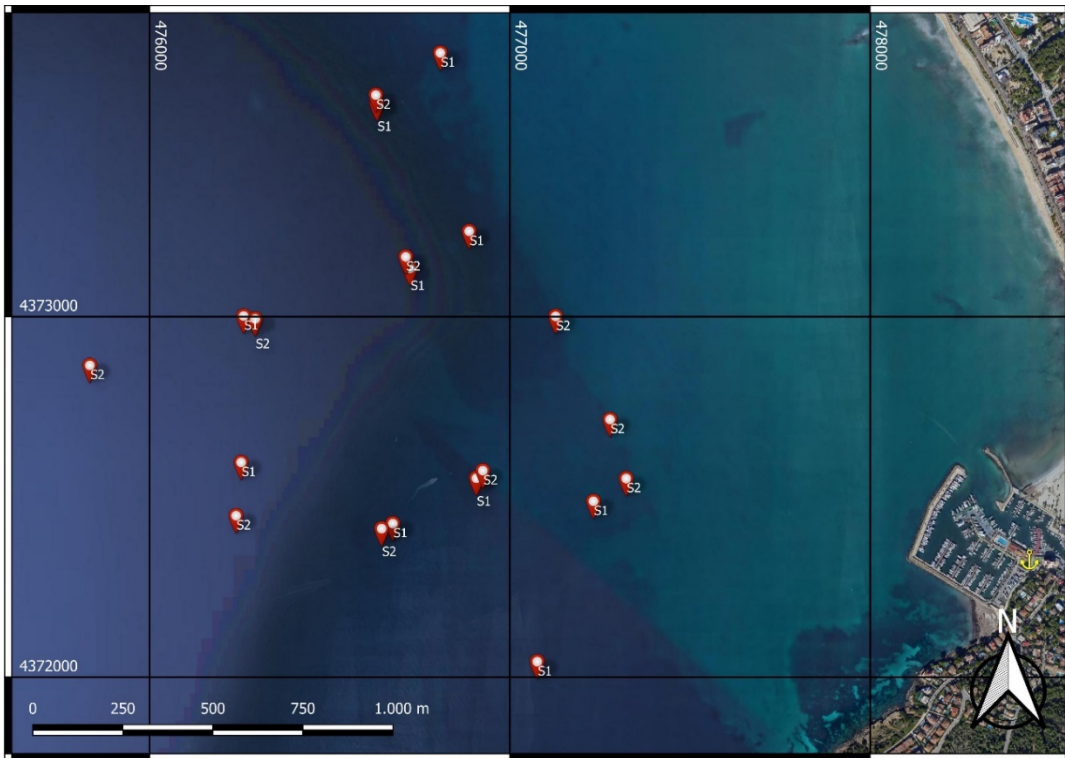
E)



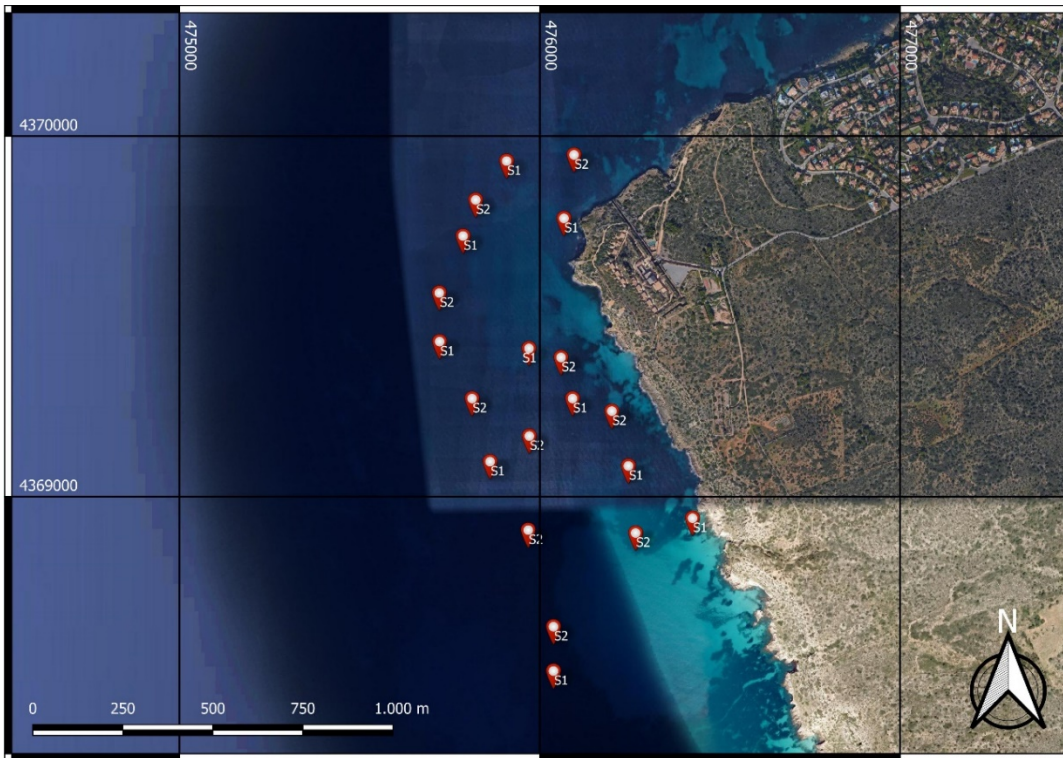
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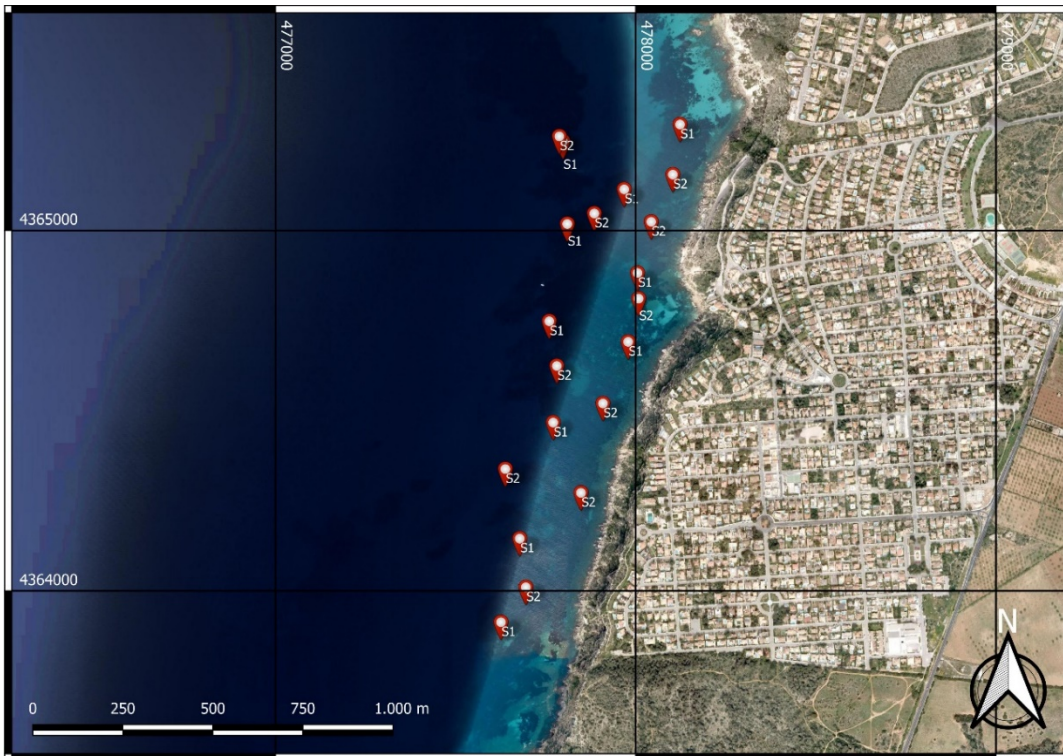
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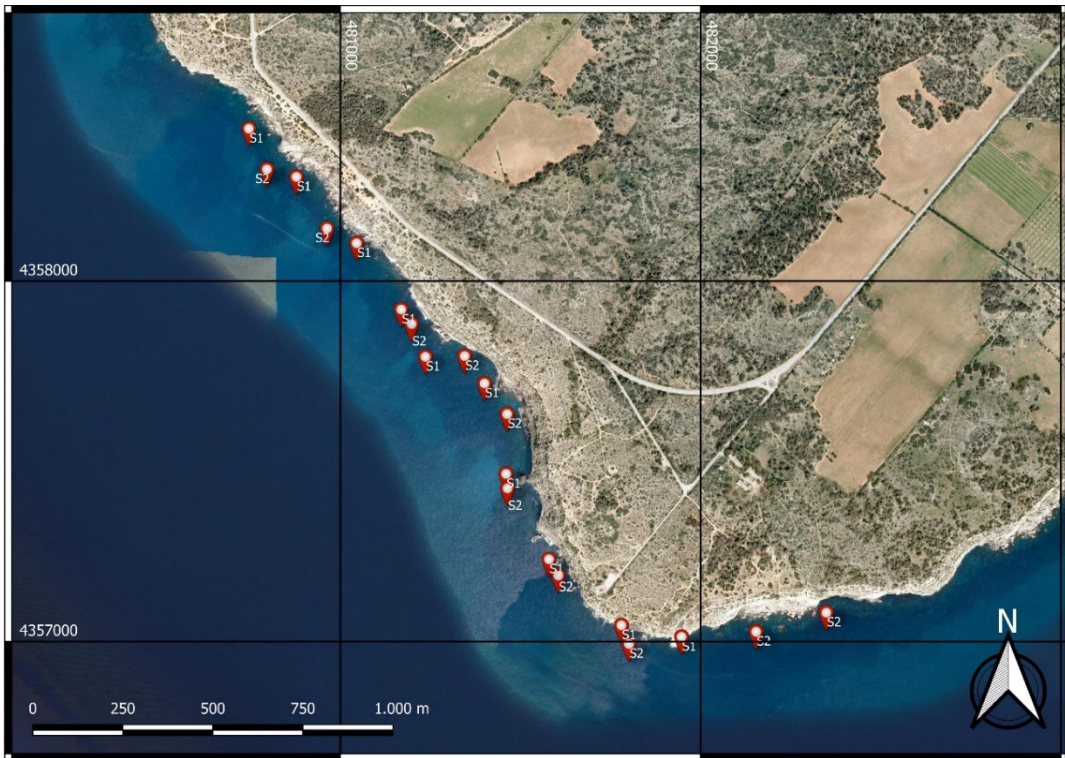
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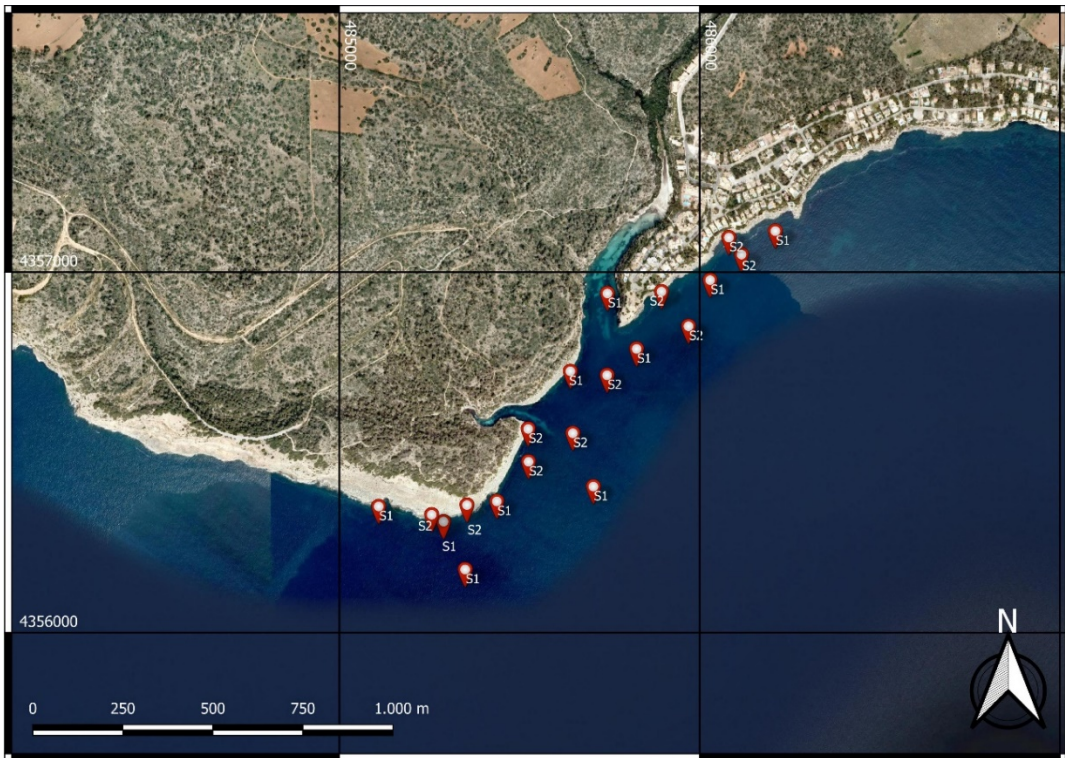
I)



J)



K)



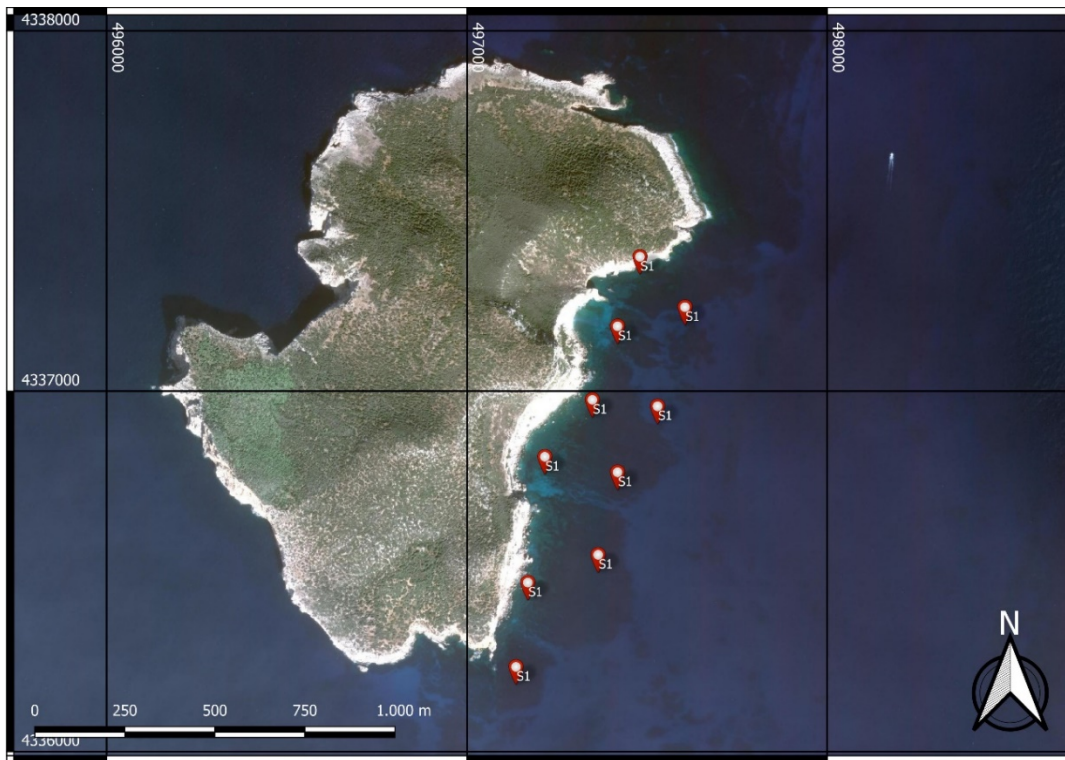
L)



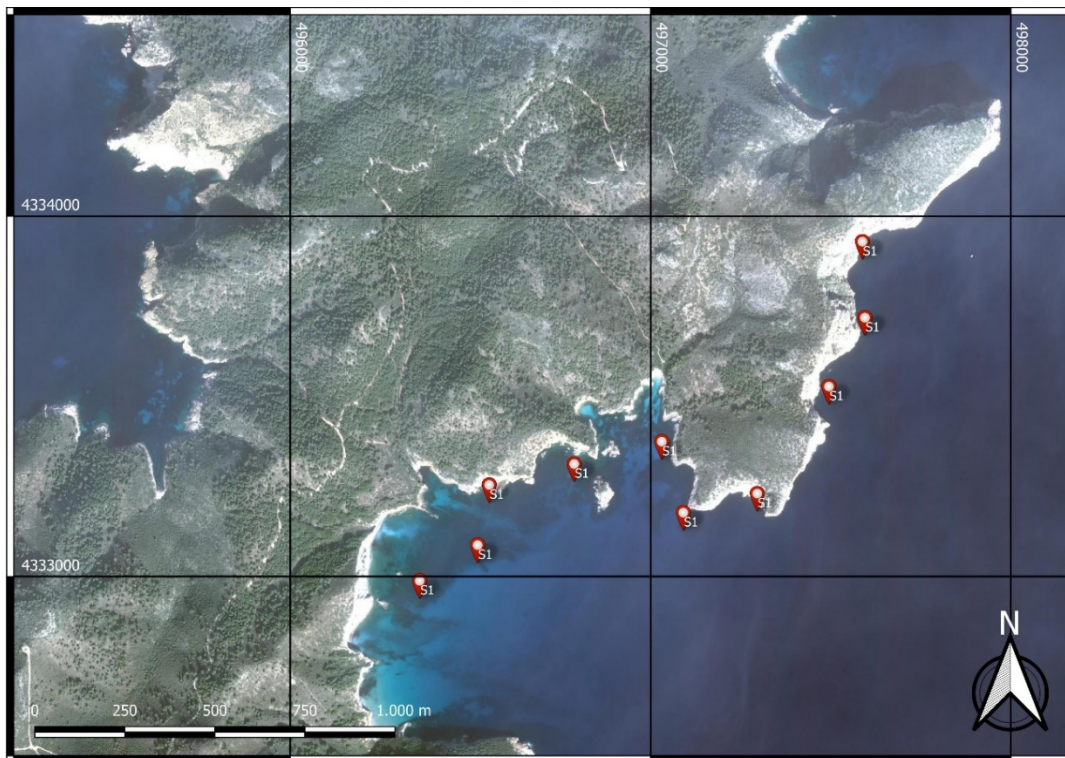
M)



N)



O)



Supplementary figure B-2. *Camera device deploying on the sea floor.*



C. Supplementary material Chapter V:

*Consequences of trait-selective fisheries on population reproductive potential:
an experimental approach.*

Supplementary figure C-1. *Example of a tank for the Experiment#1: Scoring vulnerability to angling with the camera in the surface, the hooks and line device and some Posidonia oceanica mimics.*

