ORIGINAL ARTICLE



Mesoscale productivity fronts and local fishing opportunities in the European Seas

Jean-Noël Druon¹ | Didier Gascuel² | Maurizio Gibin^{1,3} | Antonella Zanzi¹ |

Jean-Marc Fromentin⁴ | Francesco Colloca⁵ | Pierre Hélaouët⁶ | Marta Coll⁷ |

Alessandro Mannini¹ | Joanna K Bluemel⁸ | Chiara Piroddi¹ | Francois Bastardie⁹ |

Diego Macias-Moy^{1,10} | Paraskevas Vasilakopoulos¹ | Henning Winker¹ |

Natalia Serpetti¹¹ | Jordi Guillen¹ | Andreas Palialexis¹ | Michaël Gras¹ |

Zeynep Hekim¹ | Laurent Dubroca¹² | Cecilia Pinto¹ | Jeroen Steenbeek¹³ |

Jann Martinsohn¹ |

Correspondence

Jean-Noël Druon, Directorate D – Sustainable Resources, Joint Research Centre (JRC), European Commission, 21027 Ispra (VA), Italy.

Email: jean-noel.druon@ec.europa.eu

Present address

Natalia Serpetti, National Institute of Oceanography and Applied Geophysics (OGS), Trieste, Italy Cecilia Pinto, DISTAV - Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università di Genova, Genova, Italy

Abstract

This study evaluates the relationship between both commercial and scientific spatial fisheries data and a new satellite-based estimate of potential fish production (Ocean Productivity available to Fish, OPFish) in the European Seas. To construct OPFish, we used productivity frontal features derived from chlorophyll-a horizontal gradients, which characterize 10%–20% of the global phytoplankton production that effectively fuels higher trophic levels. OPFish is relatively consistent with the spatial distribution of both pelagic and demersal fish landings and catches per unit of effort (LPUEs and CPUEs, respectively). An index of harvest relative to ocean productivity (H_p index) is calculated by dividing these LPUEs or CPUEs with OPFish. The H_p index reflects the intensity of fishing by gear type with regard to local fish production. Low H_p levels indicate lower LPUEs or CPUEs than expected from oceanic production, suggesting

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 European Union. Fish and Fisheries published by John Wiley & Sons Ltd.

¹European Commission, Joint Research Centre (JRC), Ispra, Italy

²ESE, Ecology and Ecosystem Health, Institut Agro, INRAE, Rennes, France

³Consumer Data Research Centre, Department of Geography, UCL, London, UK

⁴MARBEC, IFREMER, IRD, CNRS, University of Montpellier, Sète, France

⁵Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Naples, Italy

⁶Marine Biological Association, Plymouth, UK

⁷Institute of Marine Science (ICM), Spanish National Research Council (CSIC), Barcelona, Spain

⁸Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Weymouth, UK

⁹DTU-Aqua, National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark

¹⁰Institute of Marine Sciences of Andalusia (ICMAN), Spanish National Research Council (CSIC), Cadiz, Spain

¹¹Scottish Association for Marine Science - SAMS, Oban, UK

¹²Laboratoire Ressources Halieutiques de Port en Bessin, Port en Bessin, France

¹³Ecopath International Initiative (EII) Research Association, Barcelona, Spain

over-exploitation, while high H_p levels imply more sustainable fishing. H_p allows comparing the production-dependent suitability of local fishing intensities. Our results from bottom trawl data highlight that over-exploitation of demersal species from the shelves is twice as high in the Mediterranean Sea than in the North-East Atlantic. The estimate of H_p index by dominant pelagic and demersal gears suggests that midwater and bottom otter trawls are associated with the lowest and highest overfishing, respectively. The contrasts of fishing intensity at local scales captured by the H_p index suggest that accounting for the local potential fish production can promote fisheries sustainability in the context of ecosystem-based fisheries management as required by international marine policies.

KEYWORDS

 ${\it catches per unit of effort, chlorophyll-} a {\it gradient, landings per unit of effort, local-scale,} \\ {\it Plankton-to-fish estimate, spatial fisheries management} \\$

1 | INTRODUCTION

Understanding the intertwined dynamics of marine ecosystems and fishing activities is key to implementing an effective ecosystem approach to fisheries management (Hernvann et al., 2020; Jennings et al., 2012; Tam et al., 2017). Spatial heterogeneity in environmental variables, such as salinity, temperature, or chlorophyll-a, govern species distributions and shape the predator-prey relationships throughout the food web (Kortsch et al., 2019; Polis et al., 1997). Also, seabed features and water column characteristics mediate species interactions determining the structure and functioning of marine ecosystems (Gravel et al., 2011; Libralato et al., 2014). Finally, benthic habitats play an essential role in the spatial variability of marine food webs and exchanges between the pelagic and benthic compartments of ecosystems through food accessibility and trophic transfer efficiency (Agnetta et al., 2019; Stock et al., 2017).

Fishers typically tend to adapt to this natural distribution of marine resources by attempting to concentrate their fishing effort in the most productive areas, resulting in spatially heterogeneous impacts on ecosystems (Tremblay-Boyer et al., 2011). There is thus a need for analysing the spatial distribution of fishing pressure in relation to food web productivity, to better understand the impacts of fishing on the ecosystem and integrate spatial ecology into ecosystem-based management (Baudron et al., 2020; Lowerre-Barbieri et al., 2019).

Spatial considerations are generally not included in fishery stock assessment and management because of the lack of spatially explicit data and a poor understanding of the spatial dynamics of fish populations, especially migratory ones (Fromentin et al., 2014; Gillanders et al., 2015; Morris et al., 2014). Nonetheless, by assuming that a fish stock in a management unit is randomly distributed with respect to fishing effort (Quinn & Deriso, 1999), standard stock assessments may lead to local overfishing (Maury & Gascuel, 2001). This outcome is particularly worrying for fish populations, which most often aggregate during particular life-history stages, for example, during spawning or recruitment in

1 INTRODUCTION	1228
2 MATERIALS AND METHODS	1229
2.1 The satellite-derived data and potential fish production	1229
2.1.1 Satellite-derived chlorophyll-a gradient	1229
2.1.2 The generic estimate of Ocean Productivity available to Fish (OPFish)	1229
2.2 The spatial fisheries data	1231
2.2.1 Commercial fisheries data	1232
2.2.2 Scientific fisheries surveys	1234
2.3 The gear-specific index of Harvest relative to ocean productivity (H _p index)	1234
3 RESULTS	1235
3.1 Highlights from the commercial fisheries data in the North-East Atlantic shelf	1235
3.2 Additional patterns from the scientific surveys in the North-East Atlantic and Mediterranean Sea shelves	1235
3.3 Overall features of the share by gear in extracting local potential fish production	1237
4 DISCUSSION	1237
4.1 Consistency of results versus limitations	1237
4.2 The adaptation of fishing fleets to fish production is a matter of local scale	1241
4.3 Perspectives for research, management and policy	1241
5 INTRODUCTION TO THE SUPPLEMENTARY INFORMATION	1243
ACKNOWLEDGEMENTS	1243
CONFLICT OF INTEREST	1243
DATA AVAILABILITY STATEMENT	1243
REFERENCES	1244

nursery habitats (Beck et al., 2001; Claydon, 2004). After a contraction of their feeding or reproduction habitat, the aggregating populations may be more accessible to fishing (Druon et al., 2017). Dynamic protection of these habitats can benefit exploited populations (Chollett et al., 2020; Grüss et al., 2019), increase the resilience of fisheries facing climate change (Rassweiler et al., 2012), and optimize bioeconomic trade-offs (Oyafuso et al., 2019). Therefore, spatial fisheries management is needed to adjust the local fishing activity to local fish production, thereby improving sustainability. This management involves efficient spatial zoning for fisheries and conservation (Kaplan et al., 2012; Li et al., 2020; Neat et al., 2014) in order to evolve from standard stock-based management to integrated fleet-based management (Gascuel et al., 2012).

New powerful tools based on satellite-derived data, such as fishing activity at fine spatial scales (e.g. bottom trawl fishing footprints, Amoroso et al., 2018) and/or phytoplankton distribution (Chassot et al., 2010; Hartog et al., 2011; Saitoh et al., 2011), have been developed over the last decades (Chassot et al., 2011). These tools have opened the door for a spatialized ecosystem approach to fisheries management. However, to our knowledge, no analysis has been attempted to compare spatial fisheries data to a satellite estimate of plankton-to-fish production at a fine scale, highlighting through this process the complementarity of commercial versus. scientific data.

In this paper, we investigate the relationship between a new estimate of potential fish production, derived from satellite remote sensing of productivity fronts (the Ocean Productivity available to Fish, hereafter OPFish), and catch or landings per unit of effort (CPUEs and LPUEs, respectively) in European Seas. We detail the links between productivity fronts, mesozooplankton and the feeding of higher trophic levels. We then use spatial fisheries data sets with different attributes to build a second index, the Harvest relative to ocean productivity (hereafter H_p index). This H_p index is defined as the ratio of gear-specific CPUEs or LPUEs over the potential fish production (OPFish). Hp index aims to evaluate if the fishing intensity of each fleet segment is proportionate to the local fish production. Low H_D levels indicate lower LPUEs or CPUEs than expected from the oceanic production available to fish, suggesting over-exploitation, while high H_D levels imply more sustainable fishing

The distribution of the H_p index is discussed across spatial scales, regional seas, main gear types and fisheries data attributes. Finally, we examine the implications of the H_p index and such a spatial approach for research, fisheries management and international marine policies.

2 | MATERIALS AND METHODS

This study seeks to explore the variability of fishing capacity against a novel estimate of potential productivity across the European Seas, with a strong emphasis on the importance of scales in fisheries management. Our approach involves comparing different types of spatial fisheries data with this new proxy for the fisheries-independent

potential production of fish (OPFish). As a result, commercialderived LPUEs, at two different spatial resolutions, and CPUEs from scientific surveys, were associated with the estimate of potential fish production coherently integrated in space and time.

2.1 | The satellite-derived data and potential fish production

2.1.1 | Satellite-derived chlorophyll-a gradient

Daily chlorophyll-*a* (mg.m⁻³) data were gathered from the MODIS-Aqua ocean colour sensor (2003–2016; 1/24° resolution) using the Ocean Color Index (OCI) algorithm (Hu et al., 2012) and extracted from the NASA portal (https://oceancolor.gsfc.nasa.gov/I3/) with the archive reprocessing of January 2018. MODIS-Aqua is the only active ocean colour sensor covering the equivalent period to the used commercial fisheries data (mostly 2010–2016). The daily chlorophyll-*a* data were preprocessed using iterations of a median filter to recover missing values on the edge of the valid data, followed by a Gaussian smoothing procedure to remove eventual sensor stripes (Druon et al., 2012, 2021). The norm of the chlorophyll-*a* gradient (*gradCHL*) was derived from the daily chlorophyll-*a* data, using a bidirectional gradient over a three-by-three grid-cell window as follows:

$$gradCHL = \sqrt{Gx^2 + Gy^2}$$

with Gx, Gy, the longitudinal and latitudinal chlorophyll-a horizontal gradient, respectively, corrected by the pixel size in km. Small and large chlorophyll-a fronts refer to variable levels of chlorophyll-a gradient values (see the first section of the Supplementary Information, hereafter S.I.). The gradCHL values, which are linked to the presence of pelagic species, were used in log-form to derive a dependent linear function (C_g see Figure S2), which is the main component of Ocean Productivity available to Fish (OPFish).

2.1.2 | The generic estimate of Ocean Productivity available to Fish (OPFish)

OPFish is a novel estimate of plankton-to-fish production that uses the daily detection of productive oceanic features (chlorophyll-*a* fronts) from ocean colour satellite sensors (currently MODIS-Aqua) as a proxy for food availability to fish populations. Being active long enough (from weeks to months) to allow the development of mesozooplankton populations (Druon et al., 2019), productivity fronts were shown to attract pelagic fish, top predators (Briscoe et al., 2017; Druon et al., 2016, 2017; Olson et al., 1994; Panigada et al., 2017; Polovina et al., 2001) and also demersal species (Alemany et al., 2014; Belkin, 2021; Druon et al., 2015). After a first development phase of productivity fronts (3–4 weeks, Druon et al., 2019),

the substantial levels of mesozooplankton biomass reached in the resilient chlorophyll-a fronts may represent concomitant feeding hotspots for the pelagic ecosystem, with the active aggregation of highly mobile predators (e.g. bluefin tuna in Druon et al., 2016; fin whale in Panigada et al., 2017). Since about 80% in upwelling areas, 85% in coastal and 90% in oceanic waters of the phytoplankton production are remineralized and lost for higher trophic levels (Libralato et al., 2008; Raymont, 1980), the chlorophyll-a front-derived OPFish represents the carrying capacity of the ecosystem that sustains the productivity of fish species, that is, a global index of marine ecosystem productivity. The impacts of other abiotic factors on fish reproduction, which also condition their distribution, are not global but species-specific. For instance, the impact of temperature will differently affect the distribution and reproduction of Atlantic cod (Gadus morhua, Gadidae), haddock (Melanogrammus aeglefinus, Gadidae) or sardine (Sardina pilchardus, Clupeidae). As it is not currently possible to consider the species-specific impacts of multiple abiotic factors in a single index, OPFish considers only food availability. However, we consider the potential limitations of such a global index in the discussion.

The OPFish was computed daily in each grid cell using (i) a linear function derived from the horizontal gradient of chlorophyll-a of value from 0 to 1 (C_g , see Figure S2), (ii) a range of chlorophyll-acontent, with a value of 1 if in the suitable range and 0 otherwise (C_c), and (iii) the relative day length duration (DL between 0 and 1) depending on latitude and day of the year. The linear function C_{α} is defined using the minimum and spread (maximum slope of the cumulative distribution function) of the chlorophyll-a gradients associated with pelagic species presence to effectively link specific productive fronts to potential feeding (see S.I.). The OPFish was therefore bounded, at its lower limit, by the minimum size of influential productivity fronts (minimum chlorophyll-a gradient and content) and, at its upper limit, by the maximum chlorophyll-a content. This maximum chlorophyll-a level prevents a potential bias by eutrophication (disruption of the food chain) or chlorophyll-a overestimation in coastal areas due to the presence of particulate suspended matter or dissolved organic matter (Gohin et al., 2002). Weighting the OPFish by day length (in relative levels, i.e. 0 for permanent night-time and 1 for permanent daytime) accounted for the time that these productivity fronts were effectively active daily, which is highly different between seasons and from the equator to the poles. Hence, the OPFish relates to a notion of relative productivity available to high trophic level organisms (see also the S.I., for methodology details and Druon, 2017 for an application in the Arctic).

The OPFish has daily values from 0 to 1 following the equation:

$$OPFish = C_q * C_r * DL$$

where OPFish = Ocean Productivity available to Fish (potential fish production in relative level),

 C_g = linear function derived from the horizontal gradient of chlorophyll-a, from 0 to 1.

(see daily habitat index in Figure S2),

 $C_{\rm r}={\rm value}~1$ if within the suitable chlorophyll-a range, and 0 otherwise,

DL = relative day length duration from 0 to 1 (day length in hours divided by 24).

The minimum values of the chlorophyll-a gradient (gradCHL) and the range of chlorophyll-a content (CHL) suitable for each of the studied species or group of species were derived using specific cluster analysis (see Table S1, and publications herein). The species or group of species used are mesozooplankton (the 131 most present taxa in the North Atlantic, Druon et al., 2019, in press), sardine (Sardina pilchardus, Clupeidae, unpublished), anchovy (Engraulis encrasicolus, Engraulidae, unpublished), vear-0 hake (Merluccius merluccius, Merlucciidae, Druon et al., 2015), skipjack tuna (Katsuwonus pelamis, Scombridae, Druon et al., 2017), juvenile and adult Atlantic bluefin tuna (Thunnus thynnus, Scombridae Druon et al., 2016), fin whale (Balaenoptera physalus, Balaenopteridae, Panigada et al., 2017) and small juveniles and large female juveniles of blue shark (Prionace glauca, Carcharhinidae, in prep.) (see Figure S1 and Table S1). The linear function used in OPFish translated a chlorophyll-a gradient (in log scale) into a continuous variable between 0 and 1, to account for the various feeding opportunities existing between the small and large productivity fronts (see daily habitat index in Figure S2). The linear function was defined using the selected gradCHL minimum value and the maximum slope of the cumulative distribution function of all the species mentioned above, which were clustered in classes to ensure a balanced representation among trophic levels (see Figure S2). The species were clustered with equal weightings, and the classes were selected as follows: (i) mesozooplankton, (ii) small pelagic species (sardine and anchovy), (iii) age-0 fish (hake), (iv) large predators (tuna species) and top predators (fin whale and blue shark). Some life stages that were not dominantly feeding in the upper water column, thus in relation to productivity fronts, were excluded from the linear function computation. These include the adult bluefin tunas in the Mediterranean Sea, which were generally attracted by relatively poor environments for spawning, and the adult and large juvenile blue shark males, which exhibited feeding typically in mesopelagic environments. The OPFish was consequently built to refer to marine ecosystem feeding hotspots, mainly in the epipelagic layer (ca. 0-200 m), and used hereafter as a proxy of the potential fish production of pelagic species and, in the shelf area, for demersal species. It is noteworthy that the distribution of demersal fishing fleets and fishing effort were positively associated with semipermanent chlorophyll-a frontal zones (Alemany et al., 2014). Despite this, the link is more direct for pelagic fisheries (see Section 3). Daily OPFish values varied from 0 in permanent night-time near the poles, or in the absence of productivity fronts, to 1 in permanent daytime near the poles, in the presence of large fronts. Monthly mean values of OPFish were computed using the daily values and expressed in the frequency of favourable occurrence (from 0% to 100%). For the analysis, the annual OPFish was averaged in time (from the monthly mean values) to represent the potential feeding conditions of the fish present in the fisheries data. Figure 1 presents an overview of the OPFish multiannual mean over

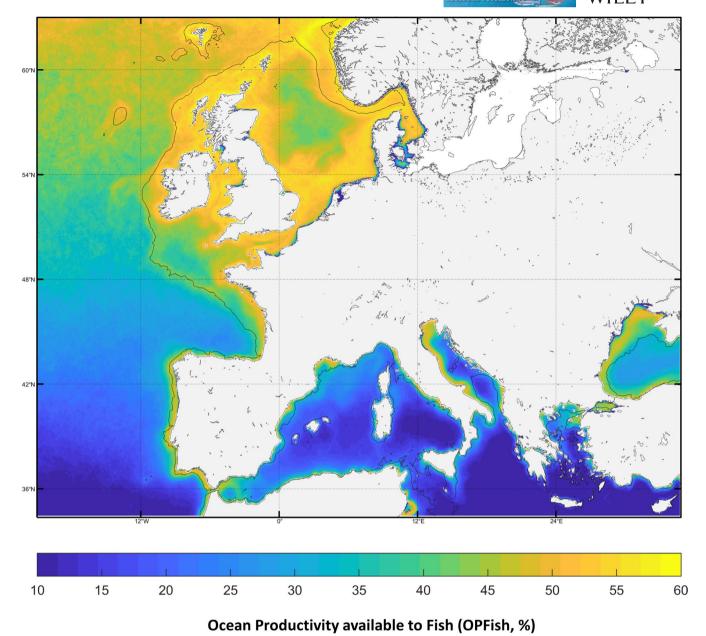


FIGURE 1 Distribution of the estimate of potential fish production, the Ocean Productivity index available to Fish (OPFish), in the European Seas as a mean value for 2003–2015 (expressed in % of daily favourable occurrence, 1/24° by 1/24°). High OPFish levels result in the frequent presence of large productivity fronts in long day length and intermediate chlorophyll-*a* levels (0.08–11.0 mg/m³, see text and S.I.). The 200 m depth contour is shown. Seasonal maps of OPFish are shown in Figure S3 in the Supplementary Information

the period 2003–2015 at the original resolution ($1/24^{\circ}$ by $1/24^{\circ}$), showing the variability in the European Seas (see the Figure S3 for the seasonal variability). Due to an overestimation of chlorophyll-a caused by dissolved organic substances in the Baltic Sea, this region was omitted from the analysis.

2.2 | The spatial fisheries data

The spatial fisheries data comprise gridded commercial landings and effort as well as local and higher precision data from scientific surveys (Figure 2). While the pelagic gear fisheries data have a more direct link with surface plankton production, we also analysed the demersal fisheries component in the shelf area (see also Section 4) because (i) the link is shown in the shelf area for demersal resources (our results), (ii) this is an essential complementary component of fish extraction, (iii) demersal fish are less mobile thus catches within a spatial cell are more likely corresponding to the observed plankton production and (iv) only large-scale scientific demersal data were available (with higher precision but lower volume and coverage than commercial fisheries data). In this study, LPUEs were solely derived from commercial data (noting

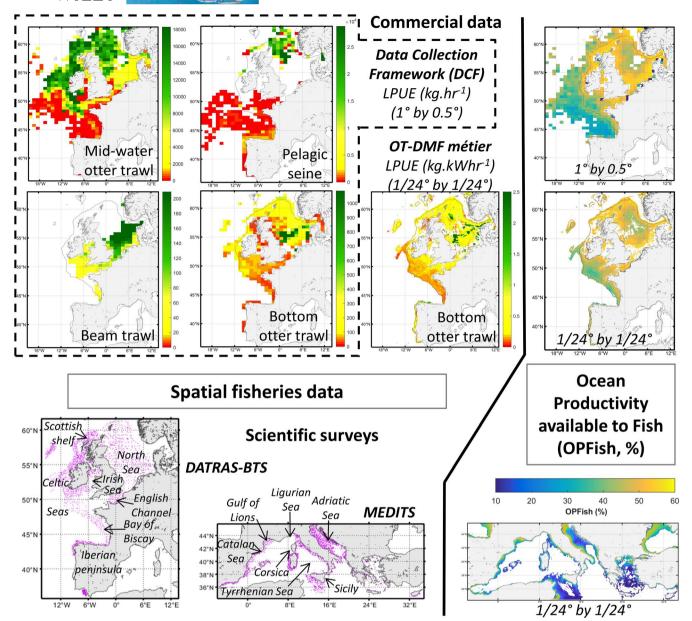


FIGURE 2 Distribution of the commercial and scientific spatial fisheries data by main gear in the North-East Atlantic and the Mediterranean Sea and OPFish at the corresponding spatial resolutions (DCF data at 1° by 0.5° [2010–2016], OT-DMF métier [2009–2016] and scientific data [2003–2016 for DATRAS-BTS and 2003–2015 for MEDITS] at 1/24° by 1/24°). The mean interannual landings per unit effort (LPUEs) are presented for the commercial fisheries data, together with the corresponding OPFish levels (0-500 m for bottom-contact gears), while only the locations of bottom trawl CPUEs are shown for scientific surveys. All bottom-contact gear data are limited to water depths lower than 500 m. The OT-DMF métier relates to bottom otter trawl data targeting demersal species from the ICES Working Group on Spatial Fisheries Data (WGSFD)

that discarded fish were not accounted for) while CPUEs only originated from scientific survey data.

2.2.1 | Commercial fisheries data

Two types of commercial fisheries data at different spatial resolutions were used. The coarser resolution data (1° by 0.5°) of the EU Data Collection Framework (hereafter DCF) are fisheries data declared by the EU Member States in the North-East Atlantic area,

thus explaining the absence of data from Norway at the margin of our area of interest. Since this data set expressed the effort in fishing hours, we only selected the data for the main fishing fleet (vessels over 15 m length) to limit the bias when comparing large (above 30 m) and small (below 10 m) vessels LPUEs. The fisheries data were largely dominated by the over 15 m length vessels compared to the 10–15 m length category for the considered gears, with 3- to 10-fold higher total effort in hours, 15- to 71-fold higher total landings, 4- to 58-fold higher maximum local LPUE (kg/hr) and two to sixfold higher ocean coverage (see Table S2). The

selected period from 2010 to 2016 corresponded to the highest quality data after the introduction in 2011 of quality checks during the data submission procedure by the EU member states (DCF data call, STECF, 2016). Because of their different spatio-temporal dynamics, we separated the bottom gear landings by pelagic and demersal species (the latter being retained) as species information was available (see the DCF species details in Tables S4 and S5). The main gears were considered separately, namely pelagic seine and midwater otter trawls for pelagic species and bottom otter and beam trawls for demersal species, to avoid effort comparison issues between gears (Figure 2). The quarterly data of fishing effort (expressed in hours), and landings (in tonnes), were aggregated into annual data.

Higher resolution data (1/20° by 1/20°) of fishing effort (which include the vessel power and hours, in kWHr) and landings (in tonnes) resulted from the geolocation of fishing events using the precise positions of the vessel monitoring system (VMS, including the vessel speed) and logbook declarations (ICES, 2019 and herein). These data were available by year, from 2009 to 2016, referring to fishing vessels above 12 m length by métier. We selected the data for the bottom OTter trawl—DeMersal Fish species (hereafter OT-DMF métier, Figure 2) as it dominated the nine métiers targeting demersal species (68% of landings and 43% of effort). This métier, covering 24% of the North-East Atlantic shelf, targeted cod (*Gadus morhua*, *Gadidae*), plaice (*Pleuronectes platessa*, *Pleuronectidae*) and Norway

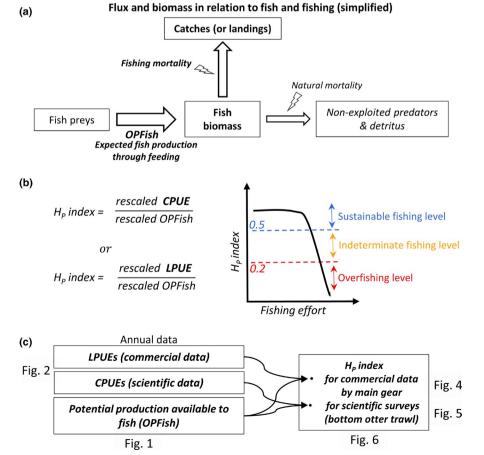
pout (*Trisopterus esmarkii*, *Gadidae*), but the species composition of hauls was unknown. The original data were provided by countries neighbouring the North-East Atlantic shelf except for Norway, the Faroe Islands and Spain. These data were re-gridded from the 1/20° by 1/20° to the grid of the satellite remote sensing data at 1/24° by 1/24° resolution.

FISH and FISHERIES

The low fishing effort values (below the 20th percentile) from both commercial fisheries data sets were filtered out to remove a potentially important bias. These low effort levels, which are more sensitive to errors than high levels, can, in turn, induce large errors of LPUEs (when calculating the ratios) while remaining relatively marginal data. Both bottom gear data (high and low resolutions) were limited to the shelf and upper slope area (lower water depths than 500 m) to limit spatial distortion in LPUE levels due to the existing link between fishing depth and vessel power. This depth filtering removed another 12% and 4% of the original data sets for the DCF bottom trawl and OT-DMF métier, respectively, and none for the DCF beam trawl.

An important aspect linking LPUEs with OPFish is their respective integration in time. The OPFish was integrated from 10 to 25 months before the last month of each year to investigate the relationship with the annual LPUEs. The assessment showed a common first peak of correlation across the commercial fisheries data by gear at about 12 months (Figure S5). This integration time was selected for OPFish to perform the comparison with the fishing LPUEs.

FIGURE 3 Schematic representation of (a) flux and biomass in relation to fish and fishing and of (b) the index of Harvest relative to ocean productivity (Hp index), that is, the annual ratio of rescaled CPUE (or LPUE) over the rescaled index of Ocean Productivity available to Fish-OPFish, and H_P dynamics with regard to fishing effort and over-exploitation and (c) workflow from spatial data to the H_D index (with the related figures' number). This ratio of CPUEs or LPUEs over an estimate of potential fish production represents the extraction of local fish production by gear. When increasing the fishing effort, the important decline of the H_D index (panel b) highlights potential overfishing where fish extraction is substantially lower than expected from potential production (see also Figure S22 for the data-corresponding representation)



2.2.2 | Scientific fisheries surveys

The purposes of using scientific survey data are (i) to compare the estimate of potential fish production (OPFish) with another data set of higher precision but lower temporal and spatial coverage than commercial data, (ii) to explore the complementarity of the information included in these two fisheries data sets and (iii) to compare the exploitation levels in the North-East Atlantic and the Mediterranean Sea shelves as, for the latter, commercial data on a regular spatial grid were currently missing. Two survey data sets of bottom otter trawl in the North-East Atlantic and the Mediterranean Sea shelves were used, DATRAS and MEDITS, respectively. Data from DATRAS bottom trawl surveys (DATRAS-BTS hereafter, https://datras.ices.dk/Home/Descriptions.aspx) were provided by countries of the North-East Atlantic area except Norway and Portugal, while MEDITS data (Spedicato et al., 2019) were provided by the EU Member States (i.e. mostly the northern basin, see Figure 2 and Figure S4). Survey data of fishing effort were available in kWHr and fishing catches in weight by species. Molluscs and true pelagic species were excluded from the survey data to focus on the targeted non-shellfish demersal species (see Tables S3 and S4 for species details). Survey data since 2003 from DATRAS-BTS (2003-2016, 7,230 hauls) and MEDITS (2003-2015, 9,415 hauls) were used as the temporal coverage corresponded to the used satellite remote sensing data (MODIS-Agua sensor since July 2002). We selected the CPUEs (kg.km⁻²) derived from the wing spread (net opening, see illustration in Figure S4) since it was available for both surveys, and the door spread (distance between the two panels preceding the net) from DATRAS-BTS was shown to be less stable comparatively (see Figure S6). The fishing net of both surveys had a codend mesh size of 20 mm. The beam length was 8 m for DATRAS-BTS and 9 m for MEDITS. Depth filtering down to 500 m was applied (as per commercial bottom gear data), leading to a reduction of 1% and 18% of the original DATRAS-BTS and MEDITS data, respectively. The OPFish was integrated from 1 to 25 months before the last month of each haul, and the variation of the correlation coefficient with CPUEs was evaluated (Figures S6 and S7). Similar to the commercial fisheries data, the first peak of correlation was at about 12 months, except in the most overfished areas (Figure S7). Therefore, the common integration time of 12 months was selected for OPFish to compare with CPUEs and LPUEs. The relationship between CPUEs and OPFish was also used to set the individual fish weight to 0.5 kg, as the correlation was higher than for lower weight limits and stable above this limit. This weight limit also favoured the comparison between DATRAS-BTS and MEDITS data since smaller fish dominate the catches in the Mediterranean Sea. An overall integration period for OPFish of 12 months (before sampling for surveys and the last month of annual commercial data) was selected (see Supplementary information for details).

2.3 | The gear-specific index of Harvest relative to ocean productivity (H_p index)

The annual ratio of rescaled CPUE (or LPUE depending on input data type) over rescaled OPFish was selected to represent an

indicator of catch per unit of effort relative to the local potential fish production (see the simplified diagram illustrating the main flux and biomass in Figure 3a). This ratio, therefore, provided information on the share of a specific gear in extracting local potential fish production and was labelled the *index of Harvest relative to ocean productivity* (*H*_n *index*):

$$Hp_{[gear,cell,\,year]} = \frac{rescaled\,CPUE\,(or\,LPUE)_{[gear,cell,\,year]}}{rescaled\,OPFish_{[cell,year]}}$$

where gear, cell and year are the gear type, grid cell and year-specific dimensions of the related variables respectively. For the same ocean productivity level (for instance, rescaled OPFish = 1), the H_D index may reach relatively high levels (value of 1) if the CPUE (or LPUE) is at the level expected from productivity (rescaled CPUE = 1), thus corresponding to likely sustainable fishing, but Hp can also have low values (e.g. 0.1) in case the CPUE (or LPUE) is much lower (rescalled CPUE = 0.1) than the same expected level from productivity, then corresponding to potential overfishing. The dynamics of the H_D index in regard to fishing effort thus describes an exploitation cycle, with maximum levels from pristine conditions to maximum sustainable exploitation at relatively low effort level, and low H_D levels in situations of over-exploitation (i.e. at high fishing effort level, Figure 3b). In the recovery phases, lower H_D levels than in pristine conditions may occur at relatively low fishing effort. The H_p index was computed for each gear by rescaling both annual values of CPUE (or LPUE) and OPFish by their respective 5th (x_{min}) and 95th (x_{max}) percentiles $(x_{rescaled} = (x - x_{min})/(x_{max} - x_{min}))$, with percentile values calculated from the distribution of all annual values and grid cells (see Figures S12 and S13). Values below the 5th and above the 95th percentiles were set to 0 and 1 respectively. Consequently, the ratio of both the rescaled components showed values mostly between 0 and 1 but occasionally exceeded 1 (see Figures S20 and S21). This rescaling of the two components of the H_P index (LPUE or CPUE and OPFish) by the extreme exploitation and production conditions was primarily done for setting a comparable variability of both components in a relevant range prior to calculating their ratio. This ratio (H_p index) thus compares a relative range of catch per unit of effort (CPUE or LPUE) to a relative range of productivity. This rescaling also allowed buffering the extreme levels where, in particular for LPUE levels in the commercial fisheries data, values may contain substantial errors. Finally, this rescaling allowed a comparison between the H_p index levels obtained from LPUEs and CPUEs, that is, from commercial and scientific fisheries data. The H_P index was computed by main gear and by year and then averaged over the considered period (see the workflow by fisheries data in Figure 3c and the H_D index by gear type in Figure 4). To identify the H_D index levels that could be interpreted as over-exploitation and sustainable fishing, we calculated, by fleet segment, the H_P median levels by decile bins of fishing effort. We observed the effort levels for which the harvest relative to production was maintained and those for which it importantly declined, respectively, interpreted as potential sustainable fishing and over-exploitation (see Figure S22 and related text for details).

3 | RESULTS

3.1 | Highlights from the commercial fisheries data in the North-East Atlantic shelf

Boundaries of H_p level that separate potential over-exploitation ($H_p < 0.2$) from more sustainable fishing ($H_p > 0.5$) were highlighted following an important decrease of harvest relative to production beyond fishing effort levels from 50th to 70th percentile values (Figure S22). A buffer level ($0.2 < H_p < 0.5$) of higher data and interpretation uncertainties was considered, corresponding to an indeterminate status of fishing level (see the first section of discussion).

In the North-East Atlantic, the H_D index for the DCF data by main gear (1° by 0.5°) and the OT-DMF métier (1/24° by 1/24°) showed contrasting levels at both regional and local scales in terms of mean interannual values (from 2010 to 2016 and from 2009 to 2016, respectively, Figure 4). Hp exhibited generally high levels (above 0.7), thus high LPUEs in regard to productivity, for the DCF pelagic fisheries (midwater otter trawl and purse seine) in the northern part of the North-East Atlantic, while mostly low levels (below 0.1), thus low LPUEs in regard to productivity, dominated the southern domain (Figure 4a and b). The LPUE spatial coverage was substantially larger for the midwater otter trawl (Figure 4a) than the pelagic seine (absence in mid-latitudes, Figure 4b). The midwater otter trawl exhibited noticeably high H_D levels in the western Celtic Seas, mostly medium-low levels (0.1-0.4 range) in the southern North Sea, and low levels in the Irish Sea (below 0.2) (Figure 4a). The demersal gears also displayed contrasting coverages (Figure 4c-4e), with fishing by the bottom otter trawl spanning over the entire shelf area, while the beam trawl effort was mainly concentrated in the southern North Sea, the English Channel, the Irish Sea, the southeast Celtic Sea and the southern Bay of Biscay. Both demersal gears displayed high H_P levels (above 0.8) in the central North Sea, while the coastal areas showed values below 0.3 (thus high and low LPUEs with regard to productivity respectively). Generally, both gear types presented relatively low Hp levels in coastal waters compared to offshore, with an exception near the western Danish coasts ($H_p > 0.5$). The H_p index of bottom otter trawl from DCF was consistent with the high-resolution OT-DMF métier (H_D mean values calculated in the 1° by 0.5° grid with 50% minimum coverage, see Figure S20), despite the various sources of limitation (effort units, main gear vs. métier, species accounted for and spatial resolution). However, the low number of H_P values above 1 tended to be higher for the high-resolution data (Figure S20). The minor geographical discrepancies of H_P index between these two similar fisheries data at different resolutions occurred mainly in the Iberian coastal area and the Scottish shelf break (Figure 4d,e). The higher spatial H_P contrasts in the highcompared to the low-resolution bottom otter trawl data revealed that substantial variabilities of fishing intensity were smoothed in the coarser resolution data (DCF at 1° by 0.5° resolution). The corresponding productivity did not display such contrasts at a local scale (Figure 2, see also effort, landings, and OPFish distributions in Figures S17 and S18). These local contrasts of LPUEs with regard to productivity mainly occurred in the central North Sea and south-west Celtic Seas (Figure 4d,e). Overall, Hp levels largely varied with LPUEs and OPFish. Low LPUEs among the examined gears appeared to occur mainly in shallow and productive waters near shore and in relatively unproductive areas off the shelf for pelagic species (Figure 2), both resulting in low H_D levels (Figure 4). By contrast, high H_D levels for the midwater trawl (Figure 4a) resulted from the highest LPUEs off the shelf of Scotland and Ireland with medium levels of OPFish (in the range from 35% to 45%, Figure 2). Correlation levels between LPUE and OPFish appeared to be higher for the pelagic than for the demersal gear data at the same spatial resolution, and for the higher resolution data when comparing the DCF and OT-DMF métier bottom otter trawl data (Figure S5).

3.2 | Additional patterns from the scientific surveys in the North-East Atlantic and Mediterranean Sea shelves

The mapped H_D index for the scientific bottom trawling surveys (Figure 5a, mean value represented per grid cell of 1/4° by 1/4°) displayed highly contrasting levels at both local and regional scales in the North-East Atlantic and the Mediterranean Sea shelves (2003-2016 DATRAS-BTS and 2003-2015 MEDITS surveys respectively). These spatial contrasts primarily resulted from the variable impacts of commercial fishing efforts in regard to the local potential fish production. Moreover, these spatial contrasts may be reinforced by mean H_p values computed from a limited number of hauls with frequent high year-to-year CPUE variability. The level of correlation between the DATRAS-BTS CPUEs with OPFish (Figure S6) was about halfway between the levels of correlation obtained for the high- and lowresolution commercial bottom trawling data with OPFish (Figure S5). In the Mediterranean Sea, a negative link (Figure S7 and 5b) was displayed for the entire basin. The highest correlation levels were, however, observed for the Geographic Sub-Areas (hereafter GSAs) 8 and 6 (Corsica-see Figure 5c and the Catalan Sea-Figure S19) with correlation coefficient r values in Corsica similar to the equivalent survey data in the North-East Atlantic (DATRAS-BTS). The lowest correlation values, which likely display particularly high local commercial fishing relative to productivity, were found for the GSAs 9, 10 and 16 (Ligurian and Northern Tyrrhenian Sea, South and Central Tyrrhenian Sea and south of Sicily respectively) (see Figure S19 for a description by GSA). The median CPUE level for the Corsica area (952 kg/km²) was similar to the median value obtained in the North-East Atlantic shelf (1,083 kg/km²) despite nearly half the median level of OPFish (median potential fish production of 26% vs. 49% respectively). Conversely, for the entire Mediterranean basin, the median CPUE level of 277 kg/km² corresponded to less than one-third of the median CPUE of Corsica despite similar median productivity levels (of 32% vs. 26% respectively).

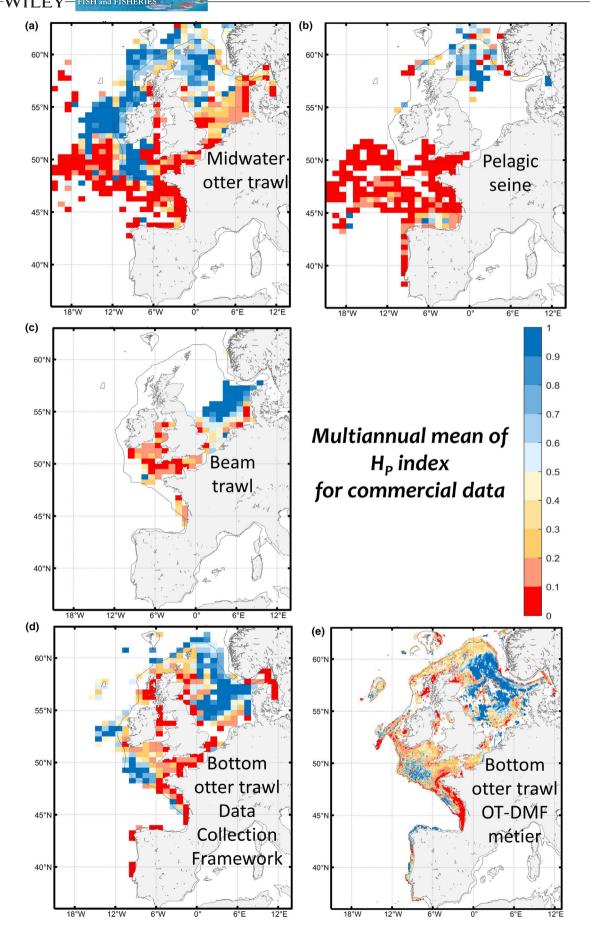


FIGURE 4 The multiannual mean of the H_p index (ratio of LPUE over the potential fish production—OPFish—both in relative levels) for (a) midwater otter trawl, (b) pelagic seine, (c) beam trawl, (d-e) bottom otter trawl. Note that the pelagic seine is largely dominated by midwater otter trawl in terms of landings. Fisheries effort and landings data are from the Data Collection Framework (DCF, 2010–2016) at 1° by 0.5° resolution (a-d) and from the ICES Working Group on Spatial Fisheries Data (WGSFD, OT-DMF métier, 2009–2016) at 1/24° by 1/24° resolution (e). The H_p index reflects the intensity of fishing by gear type with regard to local fish production, with low levels indicating lower LPUEs than expected from potential fish production, suggesting an overfished situation ($H_p < 0.2$), and higher H_p levels suggest more sustainable fishing ($H_p > 0.5$, see Figure S22 and text for details)

3.3 | Overall features of the share by gear in extracting local potential fish production

The boxplot of the H_D index for the main gears (including the scientific survey trawling) allowed direct comparison of their levels according to main gear and area (North-East Atlantic and the Mediterranean Sea, Figure 6). We produced boxplots corresponding to both the entire North-East Atlantic and shallower depths of the shelf area (below 500 m) for pelagic gears to allow comparison with bottom gears. Higher median levels of annual H_{p} index were found for pelagic gears over the shelf area for midwater otter trawl and purse seine (0.39 and 0.10, respectively), compared to the entire domain (median values of 0.28 and 0.05, respectively). The midwater otter trawl displayed the highest median H_P index value (0.39), while the purse seine (in the whole North-East Atlantic and shelf area) and the scientific bottom trawling in the Mediterranean Sea shelf area exhibited the lowest median levels (0.05-0.10 and 0.11, respectively). The various sources of data for bottom otter trawl (DCF, OT-DMF métier, DATRAS-BTS) with highly different number of samples (1,909, 422,235 and 7,230, respectively) showed consistent results in the North-East Atlantic shelf area displaying similar distributions and median values of H_p index (0.27, 0.28 and 0.24 respectively). However, the distribution of H_P index values was lower for the OT-DMF métier than for the DCF corresponding data (interquartile range of 0.44 and 0.58 respectively). These results, in Figure 6, are relatively buffered as they do not account for the lowest fishing effort (below the 20th percentile for the commercial data) and the extreme levels of CPUEs, LPUEs and productivity (<5th and >95th percentile, all data).

4 | DISCUSSION

The results of this study detail the link between the various spatial fisheries data sets available in the European Seas and a proxy for potential fish production, that is, the Ocean Productivity available to Fish (OPFish). This satellite-derived proxy of potential fish feeding was shown to greatly facilitate the identification of local fishing opportunities by quantifying the useful fraction of plankton production that could support fisheries catches. The $H_{\rm p}$ index, that is, the ratio of rescaled LPUEs or CPUEs and rescaled OPFish was found to be a suitable metric to describe, at a local scale, the relative exploitation status by fishing gear, and thus valuable for informing fisheries management. The robustness and limitations of the approach, the importance of scales and the perspectives for research and management are discussed below.

4.1 | Consistency of results versus limitations

One of the main limitations of the approach inherently originates from the fisheries data. The use of landings instead of total catches when comparing with the potential fish production is a significant source of bias as discarded fish are not accounted for, particularly for bottom gears where discards may be substantial (Coll et al., 2014; Damalas et al., 2018; Pauly et al., 2014). For example, an approximate Mediterranean-wide discard level has been estimated at around 18.6% (5.5% for seining nets, 15.0% for midwater trawl and 32.9% for bottom trawl) of total catches (Tsagarakis et al., 2014). The North Sea has been described as a global hotspot of discarding during the 1980s and 1990s with an estimated total discard rate in 1990 of 18% of total catches (22% of total landings), with beam trawl being responsible for half of this quantity (Garthe et al., 1996). Recent studies in the North Sea predicted a long-term decline over the period 1978-2011 in the overall quantity of fish discarded by mixed demersal fisheries, but an increase in the proportion of discards, with a shift from predominantly (~80%) roundfish to more than 50% flatfish (Heath and Cook, 2015). The situation should have progressively improved with the gradual implementation of the landing obligation from 2015 to 2019 for all commercial fisheries in EU waters (Guillen et al., 2018), although at-sea monitoring to reinforce implementation is likely needed (Borges, 2021).

Another important potential bias of commercial fisheries data lies in the uncertainty when declaring the DCF effort unit by countries (either in fishing days or hours) and in the non-declaration of the vessel power, preventing accurate comparison of fishing effort and subsequent LPUEs of vessels of various lengths and power (e.g. <10 m length compared to above 30 m length). We only used data from the vessel segment with the highest proportion of landings (over 15 m length) to mitigate this bias. The known species composition of the DCF data allowed for the removal of the true pelagic species (e.g. sardine, anchovy, see Tables S4 and S5) from the bottom gear landings so that analyses could explicitly focus on the spatiotemporal dynamics of the targeted demersal species (i.e. limited horizontal displacement and feeding location in the water column). This exclusion was not possible for the higher resolution OT-DMF data for which the species composition is unknown, although demersal species are targeted. The OT-DMF data represent the main métier for the demersal fisheries with a relatively accurate estimation of the effort in space and intensity (in kWHr) for the larger vessels (above 12 m length). The high spatial resolution of the OT-DMF métier (at 1/24° by 1/24° resolution) certainly increases the accuracy of the effort positioning compared to the DCF data (at 1° by 0.5°). However,

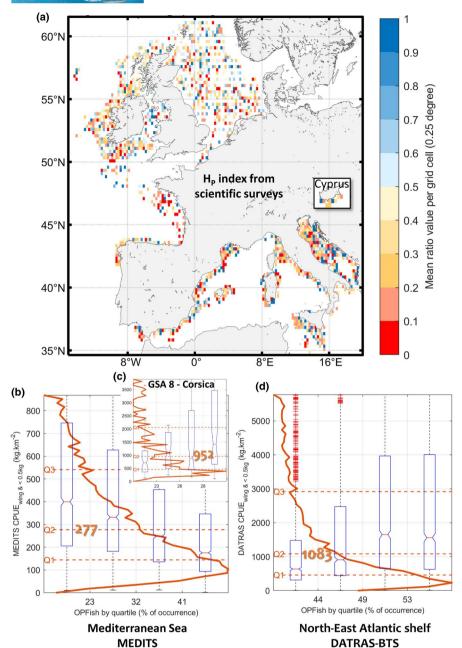
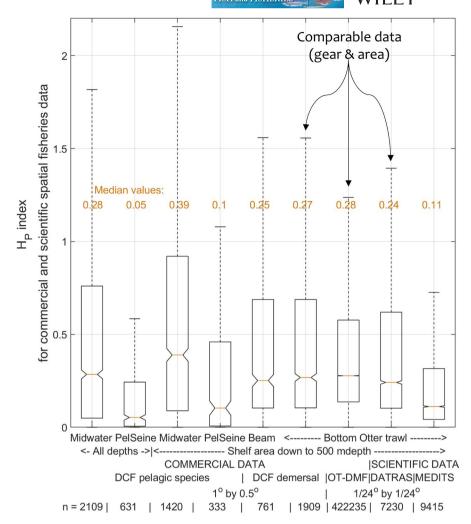


FIGURE 5 (a) Distribution of the mean H_p index (ratio of CPUE over the potential fish production—OPFish—both in relative levels) for the DATRAS-BTS (North-East Atlantic, 2003–2016) and MEDITS (the Mediterranean Sea, 2003–2015) bottom otter trawl scientific surveys (mean inter-annual value per grid cell of $1/4^\circ$ and with OPFish integrated over 12 months prior sampling). The H_p index reflects the intensity of fishing by gear type in regard to local fish production, with low levels indicating lower CPUEs than expected from potential fish production, suggesting an overfished situation ($H_p < 0.2$), and higher H_p levels suggest more sustainable fishing ($H_p > 0.5$, see Figure S22 and text for details). Boxplots of CPUEs by quartiles of OPFish (and corresponding CPUE distribution, orange line) for (b) MEDITS data in the entire Mediterranean Sea, (c) the restricted Corsica area (GSA 8) and (d) DATRAS-BTS data in the North-East Atlantic shelf. The CPUE median value is indicated for each area (Q2 in kg/km²) and interquartile range (Q1 and Q3). Differences in fishing pressure likely explain that the median value of the bottom trawl CPUEs is 3.9-fold higher in the North-East Atlantic than in the Mediterranean Sea shelves, while the median production level is only 1.5-fold higher. This relatively high median CPUE value in the Atlantic shelf is, however, similar in the Corsica area, where fishing pressure is low and median production is about twice lower, enhancing partial over-exploitation in the former and sensitivity to overfishing in the latter (see text for details)

the high-resolution data may not respect the implicit hypothesis of the analysis (using the potential fish production) that fish remain in the same cell for the considered period (one year), thus introducing some level of noise in the $H_{\rm p}$ index. This possibility may explain the

lower variability of the H_p index for the high-resolution OT-DMF compared to DCF data (Figure 6 and Figure S22). However, we observed good spatial consistency between both bottom otter trawl commercial data when integrating the high-resolution H_p index

FIGURE 6 Overall boxplot comparison of the annual H_D index distribution between commercial and scientific fisheries data by gear. The H_D index is the ratio value of CPUE or LPUE over the potential fish production (OPFish) both in relative levels. The median H_p index values are indicated for each gear (in sand colour). The estimates for the midwater otter trawl and pelagic seine are presented for the entire domain, and similar to the mobile bottom gears. for the shelf area only (down to 500 m depth). Note that the pelagic seine is largely dominated by midwater otter trawl in terms of landings. The spatial resolution and number of data samples are indicated for each gear (1/24° for the scientific data refers to the used OPFish resolution)



values in the lower resolution grid (see Figure S20). The commercial data, with large spatio-temporal coverage, undoubtedly contain representative information on the bulk biomass, which arises when comparing with the potential fish production despite inherent uncertainties (e.g. effort unit, no discards in landings, declaration errors). Comparatively, the scientific survey data are more precise (catches in kg/km², species and size compositions, haul position) but are also fundamentally more scattered in time and space. Overall, each spatial fisheries data set has limitations, including quality issues, but possesses specific positive and complementary attributes in the context of this study. Good consistency between the similar data types (bottom otter trawl from DCF, OT-DMF, and DATRAS-BTS in Figures 4 and 6) indicates that their respective robustness is suitable for use as spatial data in this study. The minor discrepancies in the Iberian coastal and Scottish shelf-break areas (Figure 4d,e) are likely due to differences in data set resolution on the edge of the domain and the missing data contribution (lack of Spanish data in the OT-DMF métier).

As an Earth-observation product, the OPFish is limited by cloud coverage, which can be particularly high in the North-East Atlantic in winter north of 45°N. This is partially mitigated using monthly means (thus of the same weight) in the annual estimates. As a proxy for potential fish production, the OPFish may be affected by (i) the variable

transfer efficiency in the food web between estimates in the oceanic waters (10%), coastal (15%) and upwelling areas (20%) (Libralato et al., 2008; Raymont, 1980), (ii) an increased uncertainty of the relationship with production in the deeper ocean and iii) the nondetection of subsurface primary production. The variable ecotrophic efficiency, that is, the variable proportion of the net annual production consumed by higher trophic levels, is to some extent captured by the level of the chlorophyll-a gradient, which was linked to the mesozooplankton biomass and subsequent duration of productivity fronts (Druon et al., 2019). To mitigate the uncertainty associated with water depth, we only retained bottom fisheries data from <500 m deep. A 200 m depth limit would have led to only accounting for on-the-shelf data in the high-resolution OT-DMF data, while shelf break data would have been included in the coarser resolution DCF data (selection using the central cell position). Even though satellite ocean colour does not detect the deep chlorophyll-a maximum, such oligotrophic environments are, however, generally considered to be substantially less productive than areas where chlorophyll-a is maximum at the surface, because of light limitation (exponential decrease of light with increasing depth). The OPFish, therefore, underestimates the natural fish production in oligotrophic environments (especially in the summer), where, in any case, fisheries data used in this study were relatively scarce (mostly in parts of the GSAs 5, 15, 22, and 25 for the MEDITS surveys, that is, parts of the Balearic Islands, Malta area, the Aegean Sea and Cyprus area, respectively, with lowest OPFish quartile values below 16%). Therefore, our results should be taken with caution in oligotrophic environments (OPFish levels below ~16%).

The OPFish only uses biotic conditions (the chlorophyll-a gradient and content) and not the abiotic factors, thus strictly focuses on the feeding capacities of the global marine ecosystem. On the one hand, regarding plankton, the abiotic conditions are implicitly considered to influence the plankton production that is captured by the chlorophyll-a gradient and content near the sea surface. On the other hand, the abiotic impacts on reproduction, which seasonally affect the distribution of most fish, are important but are temporarily restricted and specific to each species. These species characteristics cannot be included in a single index, and consequently, the lack of inclusion of reproductive behaviour remains a limitation of the approach when comparing OPFish with fisheries data. The general poleward movement of temperature-sensitive species, as generated by the warming of the surface ocean, is a process that affects most fish species. The main feeding component of this process is captured well by OPFish, whereby a warmer tolerant species replaces a colder tolerant species in a given area (e.g. in the North Sea, Engelhard et al., 2011; the temperature of the catch in the Mediterranean Sea, Tsikliras & Stergiou, 2014). However, the overall biomass observed was stable at the scale of several decades in weakly impacted ecosystems by fisheries (Bell et al., 2014), suggesting compensation dynamics in species assemblages.

Regarding the impact of using seasonal versus annual commercial landings data and OPFish on the Hp index, the results for the data available by quarter (DCF data only, results not shown) reveal very similar mean distributions of the H_B index (Figure 4) and slightly lower correlation coefficients by gear (0.2 vs. 0.29 for midwater trawl, 0.28 vs. 0.35 for pelagic seine, 0.16 vs. 0.18 for beam trawl and 0.10 vs. 0.11 for bottom trawl). These results were obtained when integrating OPFish over 12 months before the last month of the considered fisheries data, while negative correlation values were obtained when the OPFish integration was done over the same quarter period. This finding suggests that the integration over 12 months of commercial fisheries data and OPFish, as the mean period of a fish lifetime within its environment, best represents the variability of fish biomass, especially noting the high seasonality of OPFish (see Figure S3). We also chose the common integration time of OPFish at 12 months because it nearly corresponds to the month of the first correlation peak (see Figures S5-S7), marking the importance of the annual cycle (reproduction and recruitment).

The rescaling of CPUEs (or LPUEs) and OPFish, by their respective 5th and 95th percentile values, was primarily done to set comparable variability levels (between 0 and 1) in a relevant range before calculating the ratio leading to the $H_{\rm p}$ index (see Methods and Figures S12 and S13). This rescaling method prevents the most extreme levels, notably of LPUE with potential errors, from dominating the $H_{\rm p}$ distribution. However, to be robust and representative, rescaling requires the considered geographical area to include

a wide range of LPUEs (or CPUEs) and OPFish levels. Therefore, the larger the scale of the analysis, the more robust and consistent the results. Despite some H_p variability between the gears for a given level of effort (Figure S22), potential over-exploitation for H_p below 0.2, and more sustainable fishing for H_p above 0.5 appears to be reasonable boundaries considering the important decline of the harvest relative to productivity beyond the median fishing effort. These approximate boundary limits include most of the differences between fleet segments and provide a buffer range (H_p between 0.2 and 0.5), where most of the data and interpretation uncertainties are represented, corresponding to an indeterminate status of fishing level (see also S.I.).

Our results provide useful insights into the processes linking local fish production to both pelagic and demersal fisheries. The more prominent link between the potential fish production and the pelagic compared to the demersal data (DCF data, Figures S5) is likely to have two main causes. Firstly, there is a direct link between pelagic species and planktonic productivity, while the demersal species are part of a substantially more complex food web, notably involving recycling processes by detritivores. Consequently, pelagic species may primarily benefit from the plankton production in the upper water column as they represent the bulk of landed biomass (about twothirds of landings estimated from DCF data, this study). This link of plankton production with demersal species is inferior. However, the interdependency between the pelagic and demersal compartments through diurnal migration and predation ensures, to some degree, a linkage between surface production and demersal resources in the shelf area, noting that fisheries have direct and indirect impacts on that coupling (Agnetta et al., 2019). Secondly, the lower selectivity of demersal vs. pelagic gears also affects the link with potential fish production when landings are used and discards are missing. Besides these two causes, lower levels of the catch-to-productivity link are also largely generated by (i) any degree of over-exploitation (e.g. similar or lower CPUEs for the highest OPFish quartile levels from scientific surveys, Figure 5b and 5d) and (ii) the fragmentation of the available resource by gear in comparison to the overall potential fish production. This latter aspect is illustrated here by the higher LPUE-OPFish correlation for the combined compared to the individual gear relationship for the less over-exploited resource, that is, the pelagic fisheries, with an r-value of +0.38 compared to +0.29 and +0.35 for midwater otter trawl and pelagic seine respectively (Figure S24 and Figure S5). Overall, the absolute level of correlation between each gear's catches per unit of effort and the potential fish production is, therefore, multidimensional and should be interpreted with caution. The pelagic seine, for instance, is the gear for which LPUEs present the highest correlation with OPFish (Figure S5), mainly because it occurs in contrasting areas in terms of productivity and LPUE, but this correlation is also likely to be influenced by the dominance of the midwater otter trawl in terms of landings and coverage.

Beyond the above limitations, the association of different types of spatial fisheries data with a single remote sensing-based estimate of potential fish production enabled us to identify the main characteristics of fishing intensities in the European Seas. The higher link of OPFish with LPUEs or CPUEs exhibiting lower fishing intensities (areas and/or gears, Figure 5b-d, Figure S5-S7) suggests that OPFish predicts the spatial distribution of pelagic and demersal fish production relatively well. The H_P index consequently reflects the share of a specific gear in extracting potential fish production and is a reasonable indicator of the local fishing opportunities.

4.2 | The adaptation of fishing fleets to fish production is a matter of local scale

Overall, we expect robust estimates of the Harvest index relative to ocean productivity in a highly contrasted ecosystem in terms of productivity levels (and thus also in terms of sustainable CPUE or LPUE levels). We expect high H_p levels (>0.5) in lightly or sustainably exploited areas where the magnitude and distribution of fishing effort are suitably aligned to productivity, such as on the Scottish shelf for the midwater otter trawl fleet (Figure 4). Conversely, low H_p levels (<0.2) are expected in severely overfished areas with a reduction of the positive catch-to-productivity link to the point it becomes negative, meaning the higher the productivity, the lower the catch per unit of effort. This may occur where effort distribution is particularly imbalanced with local productivity (whether high or low) such as, on the shelf of the western Adriatic Sea that is under the influence of the Po River and in the productivity-poor area of the Sicily Strait (GSA 17 and 16, respectively, Figure S19). The overexploitation of productive ecosystems (OPFish above 50%) at short distances to ports and the high sensitivity of low productivity areas to fishing (OPFish below 30%) may explain the presence of low H_D index levels in shallow and relatively productive waters near shore and in relatively low productivity areas off the North-East Atlantic shelf (pelagic gears) respectively (Figure 4).

The results from the bottom trawling scientific surveys reveal that the CPUE median value is 3.9-fold higher in the North-East Atlantic (1,083 kg/km²) than in the Mediterranean Sea (277 kg/km²), while the median productivity is only 1.5-fold higher (49 vs. 32%, Figure 5b,d). The median CPUEs with regard to the potential fish production in the North-East Atlantic are thus more than twofold higher than in the Mediterranean Sea. This variability is reflected in the median of H_P index, which is 2.2-fold higher in the North-East Atlantic than in the Mediterranean Sea when using scientific survey data (0.24 vs. 0.11), and 2.5-fold higher when using the commercial bottom trawling data in the North-East Atlantic (0.28 or 0.27 vs. 0.11, Figure 6). These numbers generally agree with the higher fishing pressure in the Mediterranean Sea than in the North-East Atlantic, as illustrated by the nearly double estimated proportion of overfished stocks with levels of about 87% (n = 47) and 43% (n = 70), respectively (STECF, 2019), or 93% (n = 180) and 57% (n = 217), respectively (Froese et al., 2018), in 2016. Fishing pressure, as expressed by the ratio of current fishing mortality over the fishing mortality at maximum sustainable yield, is estimated to be more than double (2.2) in the Mediterranean Sea (2.52 for 36 stocks) than in the North-East Atlantic (1.16 for 58 stocks) in the period 2010-2016

(STECF, 2020). These outcomes are also consistent with the similar median CPUE levels in the Corsica area (952 kg/km², GSA 8) than in the North-East Atlantic shelf (1,083 kg/km²) despite the nearly half productivity level (median values of 26% vs. 49%, respectively), due to the quasi-absence of industrial fisheries in Corsica (Vespe et al., 2016). The lower median CPUE than expected from the potential production in the North-East Atlantic highlights partial overexploitation (contrasted H_D values in Figure 5a), and the high median CPUE level in the low-productive Corsica area reveals a high sensitivity to overfishing (0.2 < H_{p} < 0.7 in Figure 5a). Overall, these results agree with the major geographic divergence in stock status between northern Europe and the Mediterranean Sea (Fernandes et al., 2017). The short time series (6 or 7 years) precluded from deriving detailed trend maps of the exploitation conditions. However, the interannual changes of median H_p levels for commercial data suggest an overall improvement of the balance between catch opportunities and fish production over the period 2010-2016 in the North-East Atlantic shelf area (see Figure S23).

These regional results do not encompass the contrasting estimates of sustainable fishing at the local scale (Figures 4 and 5) due to the highly uneven distribution of the fishing pressure. This study highlights that the most appropriate spatial resolution for effort management of bottom gears is likely to be between 1/24° and 0.5° by 1° as a trade-off between fish movement and fishing effort footprint. The spatial contrast of fishing intensities is high at 1/24° resolution (Figure 4e) compared to the 1° by 0.5° resolution (Figure 4d), while the relatively low variability of the H_D index for the 1/24° resolution data (Figure S22) may highlight higher fish mobility at that resolution. Therefore, the resolution of spatial fisheries data should be high enough to account for local gear footprint and low enough to include consistent displacements of demersal species (within a grid cell for one year). The appropriate spatial resolution for effort management of bottom gears should indeed be large enough to include the main fish movements towards a more suitable and fished neighbouring area. We, therefore, suggest that 1/4° resolution is likely to be suitable for spatial fisheries data. More generally, high-resolution fishery-dependent data are perceived as integral to sustainable fisheries management, especially in a co-management context with stakeholders (Bradley et al., 2019).

4.3 | Perspectives for research, management and policy

The use of a generic spatial estimate of ocean productivity available to fish based on chlorophyll-*a* gradients and productivity fronts (OPFish) can allow advances in marine ecosystem science as (i) it provides a direct, observation-based and local estimate of secondary production in relative levels but comparable in space and time at the global scale (Druon et al., 2019, 2021), (ii) it can identify pelagic feeding hotspots for the higher trophic levels in the last two decades and in real time and (iii) it can be used operationally to increase the robustness of species habitat and full ecosystem analyses (Hernvann et al., 2020). At

this stage, the Harvest index relative to ocean productivity (H_p index) may enhance awareness that local overfishing of the pelagic or demersal species community may be linked to excessive fishing pressure compared to local productivity. Consequently, overfishing may not only affect specific fish stocks at the scale of a large management unit, as interpreted in current fisheries management. Fishing effort being highly uneven (e.g. in a management unit), the H_p index informs managers that sustainable ecosystem-based management requires to adapt fishing effort to the local ocean productivity. Fisheries management would therefore need to promote a better distribution of effort in regard to ocean productivity within a spatially explicit component.

The next step regarding research perspectives will be to compare OPFish locally and at a short timescale with acoustic data, which accurately assess the local abundance of pelagic species without the drawbacks of the missing discards in the commercial fisheries data and the relatively low time-area coverage of data from scientific surveys. Therefore, acoustic data may be more suitable for direct comparison but at a shorter timescale (e.g. monthly) because of fish movement. Such acoustic data were unavailable at such a large scale. Further developments will also be possible using DCF spatial data at 0.5° by 0.5° resolution in the Mediterranean Sea and other oceans exploited by the European fleets when a time series longer than just a few years will become available. This novel estimate of potential fish production will also be available for the global ocean allowing comparison with other spatial fisheries data sets. We expect that large fishing areas with contrasted fishing impacts will be emphasized in the future, particularly when considering the footprint of the various gears and industrial vs. artisanal fisheries.

Based on the results, we advocate that sustainable fishing can largely benefit from the combined use of spatially explicit commercial and scientific data. Both data sets analysed contain independent spatial information with complementary attributes (large data volume for the commercial data and extended sampling coverage and standardization for the scientific data) that enhance our knowledge of the exploitation status of marine resources. A redistribution of the fishing effort both at regional and local scales (Figures 4 and 5) would likely contribute to reducing overfishing, together with an effort reduction at the regional level where necessary. The present study provides further evidence that a local estimate of productivity available to fish is useful for spatialized management measures to mitigate regional or local over-exploitation. For instance, at the regional scale, this information could complement the approach of Lauria et al., (2020) in the region of the Sicily Strait, which is associated with mixed fishing grounds, by optimizing the ratio between the productivity of fisheries resources and the good ecological status of communities. At a local scale, this information could be used to redirect fishing effort from over-exploited to underutilized areas (Bastardie et al., 2019). More generally, the use of an ocean feature- and a satellite-based estimate of potential fish production contributes to the need of further connecting ocean observations with fisheries and marine ecosystems under climate variability in the frame of ecosystem-based fisheries management (Schmidt et al., 2019) and dynamic ocean management (Hobday & Hartog, 2014).

The spatial assessment approach suggested in this study is in line with the ideas at the foundation of the European Maritime Spatial Planning Directive (European Union, 2014). Maritime Spatial Planning aims at delineating when and where to carry out human activities at sea to ensure the best allocation of sea space between activities (Gimpel et al., 2015; Stelzenmüller et al., 2017). In particular, the spatial management of fisheries at a local scale will help ensure cross-border human activities at sea take place in an efficient, safe and sustainable way (Holger et al., 2018). Hence, identifying persistent areas for high productivity of exploited stocks could help to preserve the best fishing grounds for the fishing sector and those spaces that might become important fishing areas in the future, while ensuring access to other activities in different locations. Among the fished areas, the application of spatial management plans based on different sets of fishing closures in space and time can contribute to the recovery of exploited fish stocks and the increase of fisheries efficiency. By protecting parts of the fish stocks, the decrease in short-term profit for the fleet is estimated to be much lower than the one expected under a simple reduction of fishing effort (Russo et al., 2019). In practice, the impact of spatial fisheries management is also likely to be more effective than an attempt to control for a reduction in the overall fishing effort deployed at sea because the latter is known to incentivize fishers to increase their catching power in the long run (STECF, 2018). Additionally, ignoring spatial heterogeneity can lead to erroneous perception of stock status and failures in fisheries management whenever there is a mismatch between the biological population structures and the area-based stocks (Bastardie et al., 2017; Kerr et al., 2017). Simulation tests demonstrate that accurately accounting for spatial structure in stock assessments can improve model performance (Cadrin, 2020; Punt, 2019). Our results suggest that potential fish production documented per habitat type could be a mean to identify the varying spatial structure and growth rates for stock assessment, especially considering climate change and associated poleward migration of temperature-sensitive species. This generic fish production index may thus contribute to improving the balance between fishing opportunities and fleet capacity. Furthermore, the fishing effort distribution at the local scale is inevitably impacted by a fragmented bottom habitat, with nonsuitable seabed for bottom-contact gears (e.g. rocky bottom) and obstacles such as human infrastructures (e.g. pipelines, platforms and wind farms). If these factors locally act like permanent area closures and displace bottom-gear effort, this will likely be insufficient to adjust to local fish production. The overlap between the potential fish production and the habitat of endangered, vulnerable or protected species at the regional level may also provide useful information for minimizing the risk of interaction by fishing.

The global monitoring of potential fish production down to the local scale and in real time, as a predictor of fishing opportunities at year Y, knowing the status at year Y-1, is key to the resilience of food supply for the coastal communities. It furthermore helps anticipate the adaptation needs caused by the current change of climate. While the global frequency of productivity fronts appears to be stable over the period 2003–2019 despite the warming of the surface ocean, it

also shows substantial positive and negative trends at the regional scale (Druon et al., 2021). Additionally, the OPFish is one of the recently introduced products processed in real time of the *eStation* 2.0, an Earth Observation processing system (Clerici et al., 2013, https://estation.jrc.ec.europa.eu/), in support of the Global Monitoring for Environment and Security and Africa (GMES & Africa) Program that aims to address the growing needs of African countries to access and use Earth Observation data.

In conclusion, we believe that the estimate of potential fish production (OPFish) and associated H_p index can provide strategic support across policies: such as the EU Common Fisheries Policy (e.g. spatial fishing capacities, ecosystem-based fisheries management); the Marine Strategy Framework Directive (e.g. achieving Good Environmental Status through descriptor D1 pelagic habitats, D3 commercially exploited fish, D4 food webs; European Commission, 2008, 2017); the EU Biodiversity strategy for 2030; and the United Nations Sustainable Development Goal 14 ('to conserve and sustainably use the oceans, seas and marine resources for sustainable development').

5 | INTRODUCTION TO THE SUPPLEMENTARY INFORMATION

This work relies on auxiliary information necessary to deepen the understanding of the paper, and here we briefly introduce the content of the Supplementary Information. We first detail the Ocean Productivity available to Fish (OPFish), which is defined through the species and group of species-specific favourable range of chlorophyll-a fronts (species feeding habitat, Figures S1 and S2). The high seasonal variability of OPFish in European Seas is also shown here as a driver of fish potential feeding, with major differences between the shelf and open ocean and different latitudes that vary in day duration (Figure S3). The commercial fisheries data are detailed, highlighting the relative importance of the higher length vessel fleet segment (above 15 m, DCF data, Table S2) and the separation of pelagic and demersal species in the landings (DCF data) and catches (scientific surveys) of bottom-contact gears (Tables S3-S5). The variable catch-to-productivity link by fleet segment was explored using an increasing integration time of OPFish and variable minimum fish weight (scientific surveys only), with a general first correlation peak at about 12 months (Figure S5-7). The histogram by fleet segment of fishing effort (original and filtered by the 20th percentile), the corresponding landings, LPUEs and OPFish are shown (Figure S9-S13) together with the CPUEs and corresponding OPFish of the scientific surveys (Figure S12-S13). The rescaled LPUEs (or CPUEs) and rescaled OPFish by 5th and 95th percentiles used in the H_D index calculation are also overlaid (Figure S12-S13). The corresponding spatial distribution of effort, landings, LPUEs and OPFish by fleet segment is presented (interannual mean, Figure S14-S18), as well as boxplots of CPUEs vs. OPFish by Geographic Sub-Area (GSA) for the MEDITS survey in the Mediterranean Sea (Figure S19). The H_P index distribution by commercial fleet segment (with the distinction

of all water depths and shelf only for the pelagic gears) and by scientific survey is shown in Figures S20–S21 as a complementary representation of their spatial distribution in Figures 4-5. The potentially overfished areas ($H_p < 0.2$) and more sustainable fishing ($H_p > 0.5$) are enhanced through the decrease of the harvest relative to the ocean productivity available to fish when the fishing effort exceeds the 50th to the 70th percentile value (commercial data, Figure S22). The overall increase of the H_p index median value over the period 2010–2016 by fleet segment (since 2009 for OT-DMF) suggests an improved distribution of fishing effort with regard to potential fish production (Figure S23). Finally, we highlight that the combined H_p index of gears for the pelagic resource (and to a lower degree for the demersal resource) has a higher catch-to-productivity link than the H_p index derived from the individual gears (midwater other trawl and pelagic seine, Figure S24).

ACKNOWLEDGEMENTS

The authors would like to particularly thank the following people and organizations for their indirect contributions to this paper: the European Institutions and scientists for their contribution to the fisheries data collection (DATRAS-BTS, MEDITS, DCF, ICES-WGSFD), NASA Ocean Biology (OB.DAAC), Greenbelt, MD, USA, for the quality and availability of their ocean colour products. The authors sincerely thank Claire Saraux (IFREMER, France), Andrea De Felice (CNR-ISMAR, Italy) and Vjekoslav Tičina (IZOR, Croatia) for collaborating and providing acoustic data on small pelagic species that were used for the OPFish calibration (see S.I.). The authors are also thankful for the ongoing scientific collaboration on the global blue shark habitat for providing data and expertise (see S.I.). The authors are thankful to the anonymous reviewers for helping in editing the paper and providing valuable comments.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The OPFish data are available upon reasonable request and monthly composites for the European Seas are available on the JRC Data Catalogue (https://data.jrc.ec.europa.eu/). Chlorophyll-a data are available online (https://oceancolor.gsfc.nasa.gov/cgi/l3). Commercial fisheries data at 1° by 0.5° resolution are available from the STECF data dissemination website (https://stecf.jrc.ec.europa.eu/). Commercial fisheries data at 1/20° by 1/20° resolution and from the DATRAS-BTS surveys are available from ICES (http://ices.dk/data/data-portals/Pages/DATRAS.aspx). MEDITS data are available on request to the participating EU Member States (https://www.sibm.it/SITO%20MEDITS/principaleprogramme.htm).

ORCID

Jean-Noël Druon https://orcid.org/0000-0002-0824-8778
Francois Bastardie https://orcid.org/0000-0002-2669-6179
Paraskevas Vasilakopoulos https://orcid.
org/0000-0001-6263-9844

Jordi Guillen https://orcid.org/0000-0003-3705-2253
Michaël Gras https://orcid.org/0000-0001-9572-8456
Jann Martinsohn https://orcid.org/0000-0003-3407-5839

REFERENCES

- Agnetta, D., Badalamenti, F., Colloca, F., D'Anna, G., Di Lorenzo, M., Fiorentino, F., Garofalo, G., Gristina, M., Labanchi, L., Patti, B., Pipitone, C., Solidoro, C., & Libralato, S. (2019). Benthic-pelagic coupling mediates interactions in Mediterranean mixed fisheries: An ecosystem modeling approach. PLoS One, 14, e0210659. https://doi.org/10.1371/journal.pone.0210659
- Alemany, D., Acha, E. M., & Iribarne, O. (2014). Marine fronts are important fishing areas for demersal species at the Argentine Sea (Southwest Atlantic Ocean). *Journal of Sea Research*, 87, 56–67. https://doi.org/10.1016/j.seares.2013.12.006
- Amoroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., Eigaard, O. R., Bastardie, F., Hintzen, N. T., Althaus, F., Baird, S. J., Black, J., Buhl-Mortensen, L., Campbell, A. B., Catarino, R., Collie, J., Cowan, J. H., Durholtz, D., Engstrom, N., ... Jennings, S. (2018). Bottom trawl fishing footprints on the world's continental shelves. *Proceedings of the National Academy of Sciences*, 115, E10275-E10282. https://doi.org/10.1073/pnas.1802379115
- Bastardie, F., Berkenhagen, J., Bitetto, I., Callery, O., Coleman, P., D'Andrea, L., Depestele, J., Frost, H., Goldsborough, D., & Hamon, K. (2019). Workshop on Tradeoffs Scenarios between the Impact on Seafloor Habitats and Provisions of catch-value (WKTRADE2). https:// doi.org/10.17895/ices.pub.5598
- Bastardie, F., Nielsen, J. R., Eero, M., Fuga, F., & Rindorf, A. (2017). Effects of changes in stock productivity and mixing on sustainable fishing and economic viability. *ICES Journal of Marine Science*, 74, 535–551. https://doi.org/10.1093/icesjms/fsw083
- Baudron, A. R., Brunel, T., Blanchet, M.-A., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., Millar, C., MacKenzie, B. R., Nikolioudakis, N., Fernandes, J. A., & Fernandes, P. G. (2020). Changing fish distributions challenge the effective management of European fisheries. *Ecography*, 43, 494–505. https://doi.org/10.1111/ecog.04864
- Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., & Minello, T. J. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. BioScience, 51, 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICA MO]2.0.CO:2
- Belkin, I. (2021). Remote sensing of ocean fronts in marine ecology and fisheries. Remote Sensing, 13(5), 883. https://doi.org/10.3390/rs130 50883
- Bell, R. J., Fogarty, M. J., & Collie, J. S. (2014). Stability in marine fish communities. Marine Ecology Progress Series, 504, 221–239. https:// doi.org/10.3354/meps10730
- Borges, L. (2021). The unintended impact of the European discard ban. ICES Journal of Marine Science, 78, 134–141. https://doi.org/10.1093/icesjms/fsaa200
- Bradley, D., Merrifield, M., Miller, K. M., Lomonico, S., Wilson, J. R., & Gleason, M. G. (2019). Opportunities to improve fisheries management through innovative technology and advanced data systems. *Fish and Fisheries*, 20, 564–583. https://doi.org/10.1111/faf.12361
- Briscoe, D. K., Hobday, A. J., Carlisle, A., Scales, K., Eveson, J. P., Arrizabalaga, H., Druon, J. N., & Fromentin, J.-M. (2017). Ecological bridges and barriers in pelagic ecosystems. *Deep Sea Research*

- Part II: Topical Studies in Oceanography, 140, 182-192. https://doi.org/10.1016/j.dsr2.2016.11.004
- Cadrin, S. X. (2020). Defining spatial structure for fishery stock assessment. Fisheries Research, 221, 105397. https://doi.org/10.1016/j.fishres.2019.105397
- Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., & Le Pape, O. (2010). Global marine primary production constrains fisheries catches. *Ecology Letters*, 13, 495–505. https://doi.org/10.1111/j.1461-0248.2010.01443.x
- Chassot, E., Bonhommeau, S., Reygondeau, G., Nieto, K., Polovina, J. J., Huret, M., Dulvy, N. K., & Demarcq, H. (2011). Satellite remote sensing for an ecosystem approach to fisheries management. *ICES Journal of Marine Science: Journal Du Conseil*, 68(4), 651–666. https://doi.org/10.1093/icesjms/fsq195
- Chollett, I., Priest, M., Fulton, S., & Heyman, W. D. (2020). Should we protect extirpated fish spawning aggregation sites? *Biological Conservation*, 241, 108395. https://doi.org/10.1016/j.biocon.2019.108395
- Claydon, J. (2004). Spawning aggregations of coral reef fishes: Characteristics, hypotheses, threats and management. *Oceanography and Marine Biology: An Annual Review*, 42, 265–302. https://doi.org/10.1201/9780203507810-11
- Clerici, M., Combal, B., Pekel, J. F., Dubois, G., van't Klooster, J., Skøien, J. O., & Bartholomé, E. (2013). The eStation, an Earth Observation processing service in support to ecological monitoring. *Ecological Informatics*, 18, 162–170. https://doi.org/10.1016/j. ecoinf.2013.08.004
- Coll, M., Carreras, M., Cornax, M. J., Massutí, E., Morote, E., Pastor, X., Quetglas, A., Sáez, R., Silva, L., Sobrino, I., Torres, M. A., Tudela, S., Harper, S., Zeller, D., & Pauly, D. (2014). Closer to reality: Reconstructing total removals in mixed fisheries from Southern Europe. Fisheries Research, 154, 179–194. https://doi.org/10.1016/j. fishres.2014.01.013
- Damalas, D., Ligas, A., Tsagarakis, K., Vassilopoulou, V., Stergiou, K. I., Kallianiotis, A., Sbrana, M., & Maynou, F. (2018). The "discard problem" in Mediterranean fisheries, in the face of the European Union landing obligation: The case of bottom trawl fishery and implications for management. *Mediterranean Marine Science*, 19, 459–476. https:// doi.org/10.12681/mms.14195
- Druon, J.-N. (2017). Ocean Productivity index for Fish in the Arctic Ocean: First assessment from satellite derived plankton-to-fish favourable habitats. EUR 29006 EN, Publications Office of the European Union. Luxembourg, 2017, ISBN 978-92-79-77299-3, JRC109947. https://doi.org/10.2760/28033. http://publications.jrc.ec.europa.eu/repository/bitstream/JRC109947/ocean_productivity_index_for_fish_in_the_artic.pdf
- Druon, J.-N., Chassot, E., Murua, H., & Lopez, J. (2017). Skipjack Tuna availability for purse seine fisheries is driven by suitable feeding habitat dynamics in the Atlantic and Indian Oceans. *Frontiers in Marine Science*, 4, 315. https://doi.org/10.3389/fmars.2017.00315. https://www.frontiersin.org/articles/10.3389/fmars.2017.00315/full
- Druon, J.-N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., Mérigot, B., Garofalo, G., Mannini, A., Jadaud, A., Sbrana, M., Scarcella, G., Tserpes, G., Peristeraki, P., Carlucci, R., & Heikkonen, J. (2015). Modelling of European hake nurseries in the Mediterranean Sea: An ecological niche approach. *Progress in Oceanography*, 130, 188–204. https://doi.org/10.1016/j.pocean.2014.11.005. http://www.sciencedirect.com/science/article/pii/S0079661114001803
- Druon, J.-N., Fromentin, J.-M., Hanke, A. R., Arrizabalaga, H., Damalas, D., Tičina, V., Quílez-Badia, G., Ramirez, K., Arregui, I., Tserpes, G., Reglero, P., Deflorio, M., Oray, I., Saadet Karakulak, F., Megalofonou, P., Ceyhan, T., Grubišić, L., MacKenzie, B. R., Lamkin, J., ... Addis, P. (2016). Habitat suitability of the Atlantic bluefin tuna by size class: An ecological niche approach.

1245

- Progress in Oceanography, 142, 30-46. https://doi.org/10.1016/j.pocean.2016.01.002
- Druon, J.-N., Hélaouët, P., Beaugrand, G., Fromentin, J.-M., Palialexis, A., & Hoepffner, N. (2019). Satellite-based indicator of zooplankton distribution for global monitoring. *Scientific Reports*, 9, 4732. https://doi.org/10.1038/s41598-019-41212-2
- Druon, J.-N., Mangin, A., Hélaouët, P., & Palialexis, A. (2021). The chlorophyll-a gradient as primary Earth observation index of marine ecosystem feeding capacity. Copernicus Marine Service Ocean State Report, Issue 5. Journal of Operational Oceanography. https://doi.org/10.1080/1755876X.2021.1946240
- Druon, J.-N., Panigada, S., David, L., Gannier, A., Mayol, P., Arcangeli, A., Cañadas, A., Laran, S., Di Méglio, N., & Gauffier, P. (2012). Potential feeding habitat of fin whales in the western Mediterranean Sea: An environmental niche model. *Marine Ecology Progress Series*, 464, 289–306. https://doi.org/10.3354/meps09810. http://www.int-res.com/abstracts/meps/v464/p289-306/
- Engelhard, G. H., Ellis, J. R., Payne, M. R., Ter Hofstede, R., & Pinnegar, J. K. (2011). Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES Journal of Marine Science*, 68, 580–591. https://doi.org/10.1093/icesjms/fsq183
- European Commission. (2008). The Role of CFP in Implementing an Ecosystem Approach to Marine Management. Communication from the Commission to the Council and the European Parliament [SEC(2008)449] /*COM/2008/0187 final*/. Retrieved from http://eurlex.europa.eu/LexUriServ/LexUriServ.do?uri¼CELEX:52008DC018 7:EN:HTML FAO 2005. Review of the state of world marine fishery resources. FAO Fisheries Technical Paper. No. 457. (p. 235).: FAO.
- European Commission. (2017). Commission Decision (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/477/EU (Text with EEA relevance).
- European Union (2014). Directive 2014/89/EU of the European Parliament and of the Council of 23 July 2014 establishing a framework for maritime spatial planning. European Union. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32014L0089
- Fernandes, P. G., Ralph, G. M., Nieto, A., Criado, M. G., Vasilakopoulos, P., Maravelias, C. D., Cook, R. M., Pollom, R. A., Kovačić, M., & Pollard, D. (2017). Coherent assessments of Europe's marine fishes show regional divergence and megafauna loss. *Nature Ecology & Evolution*, 1, 0170. https://doi.org/10.1038/s41559-017-0170
- Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A. C., Dimarchopoulou, D., Scarcella, G., Quaas, M., & Matz-Lück, N. (2018). Status and rebuilding of European fisheries. *Marine Policy*, 93, 159–170. https://doi.org/10.1016/j.marpol.2018.04.018
- Fromentin, J.-M., Reygondeau, G., Bonhommeau, S., & Beaugrand, G. (2014). Oceanographic changes and exploitation drive the spatiotemporal dynamics of Atlantic bluefin tuna (*Thunnus thynnus*). Fisheries Oceanography, 23, 147–156. https://doi.org/10.1111/fog.12050
- Garthe, S., Camphuysen, K., & Furness, R. W. (1996). Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Marine Ecology Progress Series*, 136, 1–11.
- Gascuel, D., Merino, G., Doering, R., Druon, J. N., Goti, L., Guenette, S., Macher, C., Soma, K., Travers-Trolet, M., & Mackinson, S. (2012). Towards the implementation of an integrated ecosystem fleet-based management of European fisheries. *Marine Policy*, 36, 1022–1032. https://doi.org/10.1016/j.marpol.2012.02.008
- Gillanders, B. M., Izzo, C., Doubleday, Z. A., & Ye, Q. (2015). Partial migration: Growth varies between resident and migratory fish. *Biology Letters*, 11, 20140850. https://doi.org/10.1098/rsbl.2014.0850
- Gimpel, A., Stelzenmüller, V., Grote, B., Buck, B. H., Floeter, J., Núñez-Riboni, I., Pogoda, B., & Temming, A. (2015). A GIS modelling framework to evaluate marine spatial planning scenarios: Co-location of

- offshore wind farms and aquaculture in the German EEZ. *Marine Policy*, 55, 102–115. https://doi.org/10.1016/j.marpol.2015.01.012
- Gohin, F., Druon, J. N., & Lampert, L. (2002). A five channel chlorophyll concentration algorithm applied to SeaWiFS data processed by SeaDAS in coastal waters. *International Journal of Remote Sensing*, 23, 1639–1661. https://doi.org/10.1080/01431160110071879
- Gravel, D., Canard, E., Guichard, F., & Mouquet, N. (2011). Persistence increases with diversity and connectance in trophic metacommunities. *PLoS One*, *6*, e19374. https://doi.org/10.1371/journal.pone.0019374
- Grüss, A., Biggs, C. R., Heyman, W. D., & Erisman, B. (2019). Protecting juveniles, spawners or both: A practical statistical modelling approach for the design of marine protected areas. *Journal of Applied Ecology*, 56, 2328–2339. https://doi.org/10.1111/1365-2664.13468
- Guillen, J., Holmes, S. J., Carvalho, N., Casey, J., Dörner, H., Gibin, M., Mannini, A., Vasilakopoulos, P., & Zanzi, A. (2018). A review of the European Union landing obligation focusing on its implications for fisheries and the environment. Sustainability, 10, 900. https://doi. org/10.3390/su10040900
- Hartog, J. R., Hobday, A. J., Matear, R., & Feng, M. (2011). Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery-implications for present and future spatial management. Deep Sea Research Part II: Topical Studies in Oceanography, 58, 746–752. https://doi.org/10.1016/j.dsr2.2010.06.005
- Heath, M. R., & Cook, R. M. (2015). Hind-Casting the Quantity and Composition of Discards by Mixed Demersal Fisheries in the North Sea. PLoS ONE, 10(3), https://doi.org/10.1371/journal.pone.0117078
- Hernvann, P.-Y., Gascuel, D., Grüss, A., Druon, J.-N., Kopp, D., Perez, I., Piroddi, C., & Robert, M. (2020). The Celtic Sea through time and space: Ecosystem modeling to unravel fishing and climate change impacts on food-web structure and dynamics. Frontiers in Marine Science, 7, 1018. https://doi.org/10.3389/fmars.2020.578717
- Hobday, A. J., & Hartog, J. R. (2014). Derived ocean features for dynamic ocean management. *Oceanography*, 27, 134–145. https://doi.org/10.5670/oceanog.2014.92
- Holger, J., Bastardie, F., Eero, M., Hamon, K. G., Hinrichsen, H.-H., Marchal, P., Nielsen, J. R., Le Pape, O., Schulze, T., & Simons, S. (2018). Integration of fisheries into marine spatial planning: Quo vadis? *Estuarine*, *Coastal and Shelf Science*, 201, 105–113. https://doi. org/10.1016/j.ecss.2017.01.003
- Hu, C., Lee, Z., & Franz, B. (2012). Chlorophyll a algorithms for oligotrophic oceans: A novel approach based on three-band reflectance difference. *Journal of Geophysical Research: Oceans*, 117, 1–25. https://doi.org/10.1029/2011JC007395
- ICES. (2019). Working Group on Spatial Fisheries Data (WGSFD). ICES Scientific Reports., 1(52), 144. https://doi.org/10.17895/ices. pub.5648.
- Jennings, S., Lee, J., & Hiddink, J. G. (2012). Assessing fishery footprints and the trade-offs between landings value, habitat sensitivity, and fishing impacts to inform marine spatial planning and an ecosystem approach. ICES Journal of Marine Science, 69, 1053–1063. https://doi. org/10.1093/icesjms/fss050
- Kaplan, I. C., Horne, P. J., & Levin, P. S. (2012). Screening California Current fishery management scenarios using the Atlantis end-to-end ecosystem model. *Progress in Oceanography*, 102, 5–18. https://doi. org/10.1016/j.pocean.2012.03.009
- Kerr, L. A., Hintzen, N. T., Cadrin, S. X., Clausen, L. W., Dickey-Collas, M., Goethel, D. R., Hatfield, E. M., Kritzer, J. P., & Nash, R. D. (2017). Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. ICES Journal of Marine Science, 74, 1708–1722. https://doi.org/10.1093/icesjms/fsw188
- Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*, 42, 295–308. https://doi.org/10.1111/ecog.03443

- Lauria, V., Gristina, M., Fiorentino, F., Attrill, M. J., & Garofalo, G. (2020). Spatial Management Units as an Ecosystem-Based Approach for Managing Bottom-Towed Fisheries in the Central Mediterranean Sea. Frontiers in Marine Science, 7, 233. https://doi.org/10.3389/ fmars.2020.00233
- Li, Y., Sun, M., Zhang, C., Zhang, Y., Xu, B., Ren, Y., & Chen, Y. (2020). Evaluating fisheries conservation strategies in the socio-ecological system: A grid-based dynamic model to link spatial conservation prioritization tools with tactical fisheries management. *PLoS One*, 15, e0230946. https://doi.org/10.1371/journal.pone.0230946
- Libralato, S., Coll, M., Tudela, S., Palomera, I., & Pranovi, F. (2008). Novel index for quantification of ecosystem effects of fishing as removal of secondary production. *Marine Ecology Progress Series*, 355, 107–129. https://doi.org/10.3354/meps07224
- Libralato, S., Pranovi, F., Stergiou, K. I., & Link, J. S. (2014). Trophodynamics in marine ecology: 70 years after Lindeman. *Marine Ecology Progress Series*, 512, 1–7. https://doi.org/10.3354/meps11033
- Lowerre-Barbieri, S. K., Catalán, I. A., Frugard Opdal, A., & Jørgensen, C. (2019). Preparing for the future: Integrating spatial ecology into ecosystem-based management. *ICES Journal of Marine Science*, 76, 467-476. https://doi.org/10.1093/icesjms/fsy209
- Maury, O., & Gascuel, D. (2001). 'Local overfishing' and fishing tactics: Theoretical considerations and applied consequences in stock assessment studied with a numerical simulator of fisheries. *Aquatic Living Resources*, 14, 203–210. https://doi.org/10.1016/S0990-7440(01)01115-9
- Morris, C. J., Green, J. M., Snelgrove, P. V., Pennell, C. J., & Ollerhead, L. N. (2014). Temporal and spatial migration of Atlantic cod (Gadus morhua) inside and outside a marine protected area and evidence for the role of prior experience in homing. Canadian Journal of Fisheries and Aquatic Sciences, 71, 1704–1712. https://doi.org/10.1139/cjfas -2014-0036
- Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Ó Cuaig, M., Townhill, B., Schön, P.-J., Lee, J., & Righton, D. (2014). Movement of Atlantic cod around the British Isles: Implications for finer scale stock management. *Journal of Applied Ecology*, 51, 1564–1574. https://doi.org/10.1111/1365-2664.12343
- Olson, D. B., Hitchcock, G. L., Mariano, A. J., Ashjian, C. J., Peng, G., Nero, R. W., & Podesta, G. P. (1994). Life on the edge: Marine life and fronts. Oceanography, 7, 52–60. https://doi.org/10.5670/oceanog.1994.03
- Oyafuso, Z. S., Leung, P., & Franklin, E. C. (2019). Evaluating bioeconomic tradeoffs of fishing reserves via spatial optimization. *Marine Policy*, 100, 163–172. https://doi.org/10.1016/j.marpol.2018.11.016
- Panigada, S., Donovan, G. P., Druon, J.-N., Lauriano, G., Pierantonio, N., Pirotta, E., Zanardelli, M., Zerbini, A. N., & di Sciara, G. N. (2017). Satellite tagging of Mediterranean fin whales: Working towards the identification of critical habitats and the focussing of mitigation measures. *Scientific Reports*, 7, 3365. https://doi.org/10.1038/s41598-017-03560-9
- Pauly, D., Ulman, A., Piroddi, C., Bultel, E., & Coll, M. (2014). 'Reported' versus 'likely' fisheries catches of four Mediterranean countries. *Scientia Marina*, 78(S1), 11–17. https://doi.org/10.3989/scimar.04020.17A
- Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28, 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289
- Polovina, J. J., Howell, E., Kobayashi, D. R., & Seki, M. P. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography*, 49, 469–483. https://doi.org/10.1016/S0079-6611(01)00036-2
- Punt, A. E. (2019). Spatial stock assessment methods: A viewpoint on current issues and assumptions. Fisheries Research, 213, 132–143. https://doi.org/10.1016/j.fishres.2019.01.014
- Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford University Press.

- Rassweiler, A., Costello, C., & Siegel, D. A. (2012). Marine protected areas and the value of spatially optimized fishery management. *Proceedings of the National Academy of Sciences*, 109, 11884–11889. https://doi.org/10.1073/pnas.1116193109
- Raymont, J. E. (1980). *Plankton & productivity in the oceans*. Volume 1: Phytoplankton. Elsevier.
- Russo, T., D'Andrea, L., Franceschini, S., Accadia, P., Cucco, A., Garofalo, G., Gristina, M., Parisi, A., Quattrocchi, G., Sabatella, R. F., Sinerchia, M., Canu, D. M., Cataudella, S., & Fiorentino, F. (2019). Simulating the effects of alternative management measures of trawl fisheries in the central Mediterranean Sea: application of a multi-species bioeconomic modeling approach. Frontiers in Marine Science, 6, 542. https://doi.org/10.3389/fmars.2019.00542
- Saitoh, S.-I., Mugo, R., Radiarta, I. N., Asaga, S., Takahashi, F., Hirawake, T., Ishikawa, Y., Awaji, T., In, T., & Shima, S. (2011). Some operational uses of satellite remote sensing and marine GIS for sustainable fisheries and aquaculture. *ICES Journal of Marine Science*, 68, 687–695. https://doi.org/10.1093/icesjms/fsq190
- Schmidt, J. O., Bograd, S. J., Arrizabalaga, H., Barbeaux, S. J., Barth, J. A., Boyer, T., Brodie, S., Cross, S., Druon, J.-N., & Fransson, A. (2019). Future ocean observations to connect climate, fisheries and marine ecosystems. Frontiers in Marine Science, 6, 550. https://doi.org/10.3389/fmars.2019.00550
- Spedicato, M. T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., & Relini, G. (2019). The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Scientia Marina*, 83, 9–20. https://doi.org/10.3989/scimar.04915.11X
- STECF. (2016). Scientific, Technical and Economic Committee for Fisheries (STECF) - Fisheries Dependent Information (STECF-16-20). Publications Office of the European Union. JRC27758. https://doi. org/10.2788/502445
- STECF (2018). Scientific, Technical and Economic Committee for Fisheries (STECF)-Fishing Effort Regime for Demersal Fisheries in the Western Mediterranean Sea (STECF-18-09). JRC28359. https://doi.org/10.2760/509604
- STECF (2019). Scientific, Technical and Economic Committee for Fisheries (STECF) Monitoring the performance of the Common Fisheries Policy (STECF-Adhoc-19-01). Publications Office of the European Union. JRC116446. https://doi.org/10.2760/22641
- STECF (2020). Scientific, Technical and Economic Committee for Fisheries (STECF) Monitoring the performance of the Common Fisheries Policy (STECF-Adhoc-20-01). JRC120481. https://doi.org/10.2760/230469
- Stelzenmüller, V., Gimpel, A., Gopnik, M., & Gee, K. (2017). Aquaculture site-selection and marine spatial planning: The roles of GIS-based tools and models. In Aquaculture perspective of multi-use sites in the open ocean (pp. 131–148). Springer. https://doi.org/10.1007/978-3-319-51159-7_6
- Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W., Dunne, J. P., Friedland, K. D., Lam, V. W., Sarmiento, J. L., & Watson, R. A. (2017). Reconciling fisheries catch and ocean productivity. Proceedings of the National Academy of Sciences, 114, E1441–E1449. https://doi.org/10.1073/pnas.1610238114
- Tam, J. C., Link, J. S., Rossberg, A. G., Rogers, S. I., Levin, P. S., Rochet, M.-J., Bundy, A., Belgrano, A., Libralato, S., & Tomczak, M. (2017). Towards ecosystem-based management: Identifying operational food-web indicators for marine ecosystems. *ICES Journal of Marine Science*, 74, 2040–2052. https://doi.org/10.1093/icesjms/fsw230
- Tremblay-Boyer, L., Gascuel, D., Watson, R., Christensen, V., & Pauly, D. (2011). Modelling the effects of fishing on the biomass of the world's oceans from 1950 to 2006. *Marine Ecology Progress Series*, 442, 169–185. https://doi.org/10.3354/meps09375
- Tsagarakis, K., Palialexis, A., & Vassilopoulou, V. (2014). Mediterranean fishery discards: Review of the existing knowledge. *ICES Journal of Marine Science*, 71, 1219–1234. https://doi.org/10.1093/icesjms/fst074

Tsikliras, A. C., & Stergiou, K. I. (2014). Mean temperature of the catch increases quickly in the Mediterranean Sea. *Marine Ecology Progress Series*, 515, 281–284. https://doi.org/10.3354/meps11005

Vespe, M., Gibin, M., Alessandrini, A., Natale, F., Mazzarella, F., & Osio, G. C. (2016). Mapping EU fishing activities using ship tracking data. *Journal of Maps*, 12, 520–525. https://doi.org/10.1080/17445 647.2016.1195299

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Druon, J.-N., Gascuel, D., Gibin, M., Zanzi, A., Fromentin, J.-M., Colloca, F., Hélaouët, P., Coll, M., Mannini, A., Bluemel, J. K., Piroddi, C., Bastardie, F., Macias-Moy, D., Vasilakopoulos, P., Winker, H., Serpetti, N., Guillen, J., Palialexis, A., Gras, M., ... Martinsohn, J. (2021). Mesoscale productivity fronts and local fishing opportunities in the European Seas. *Fish and Fisheries*, 22, 1227–1247. https://doi.org/10.1111/faf.12585