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Climate Change Context of a Data-Limited Stock: The Case of Whelk (*Buccinum undatum*) in the Western English Channel

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Annexe III bis

Avant-propos

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1. Introduction

Global change is putting increasing pressure on marine ecosystems, and it is essential to understand its effects to anticipate impacts on the exploited resources (Brander, 2010 ; IPCC, 2023). Among its key drivers, the gradual warming of the oceans plays a crucial role. This steady rise in temperature, documented over the last few decades, has led to significant changes in marine and coastal ecosystems, directly affecting the physiology of marine species, most of which are ectothermic (Pörtner and Farrell, 2008; Doney *et al.*, 2012; IPCC, 2023). Its influence affects many biological processes such as reproduction, growth, spatial distribution and feeding behaviour (Pörtner and Farrell, 2008). It can also disrupt species interactions, modify benthic habitats and alter the availability of trophic resources (Pörtner and Farrell, 2008; Doney *et al.*, 2012). These changes, often cumulative, exert increasing ecological pressure on marine populations, particularly those already exploited by fisheries (Brander, 2010). Marine species now face both gradual but persistent changes in environmental conditions and short-lived extreme events such as marine heatwaves (MHWs). MHWs refer to short-term ocean temperature anomalies that are exceptionally warm compared to the expected conditions for a specific location and time. They are commonly defined as periods when sea temperatures exceed the 90th percentile of the historical mean for at least five consecutive days (Hobday *et al.,* 2016). These events can cause additional stress and amplify the effects of long-term trends such as changes in community assemblages in favour of tropical species or a decline in the size of older individuals (Thompson *et al.*, 2022; Grunditz, 2025). Understanding the impact of long-term increases in temperatures and MHWs caused by climate change is a key step in assessing the resilience of marine species (Doney *et al.*, 2012).

The case study of my master internship is the common whelk (*Buccinum undatum*), a benthic prosobranch gastropod of major commercial importance in Europe, primarily exploited in the UK and France, which together account for 75 % of world landings (FAO, 2022). In France, the fishery is mainly concentrated in the English Channel, where in 2021 it ranked 10th nationally in terms of volume and value and 2nd in terms of value (and 3rd in volume) in the Channel-North Sea region (SIH, 2022). Although stock structure has not been extensively investigated in this region, two stocks are commonly distinguished: the Western English Channel (WEC) and the Eastern English Channel (EEC). The Western stock, which has been exploited since the 1950s, currently represents over half of French whelk landings (SIH, 2024).

In this area, whelk is exclusively caught with plastic pots (bell or cylinder type) (Appendix.1), baited mainly with small dogfish, edible crabs or spider crabs (Santarelli Chaurand, 1985). The vessels, usually crewed by two or three fishers and equipped with a hydraulic winch, deploy an average of 400 pots per boat, arranged in lines of 20 to 100 units and hauled out every 24 to 48 hours (Hegron-mace *et al.*, 2017).

Since the 1990s, growth in Asian markets led to an increase in fishing effort, with landings rising from around 4,000 tonnes in 1983 to nearly 10,000 tonnes in the 1990s (Fahy *et al.*, 2000; SIH, 2024). This level remained stable for over two decades, but since 2016 catches have fallen sharply, dropping herto just 3,000 tonnes in 2024 (SIH, 2024). This abrupt decline raises serious concerns about the sustainability of the stock and the fisheries that depend on it.

Meanwhile, the average price per kilogram has risen, particularly after 2016, from less than €2 per kg to more than €4.50 per kg in 2023, offsetting the loss of volume for fishermen and maintaining the economic viability of the fishery (Appendix.2). However, a recent drop in prices, partly attributed to the increase in foreign imports (CRPMEM, 2024), is now raising serious concern among local fishermen, who face growing market instability.

Since the 2000s, several management measures have gradually been implemented to limit overfishing: minimum landing size (45 mm), daily quotas, a limit on the number of pots, seasonal closures, a licensing system and specific sorting grids (Appendix.3). Despite these measures, the number of active vessels in the WEC declined by 20% between 2009 and 2021, mainly due to the reduction in catches (CRPMEM, 2024). In October 2024, the Granville Bay whelk fishery lost its MSC certification, highlighting the urgent need of strengthening the sustainable management of this key resource in the region.

Whelk populations in the English Channel lie near the southern edge of the species' distribution range (AquaMaps, 2019) and, in the context of climate change, face both gradual increase in temperatures and marine heatwaves. Previous studies have suggested close links between temperature and key components of the whelk's life cycle (reproduction, growth, mortality) (Smith *et al.*, 2013; Hegronmace *et al.*, 2017; Borsetti *et al.*, 2021). Hence, shifting ocean conditions in the WEC may contribute to stock depletion, which coincides with the sharp decline in landings observed in recent years. In whelks, a eurythermal species but sensitive to rapid temperature changes (Smith *et al.*, 2013), such conditions may also lead to reduced activity, reduced feeding and reduced catchability, as has been suggested following the hot summers observed in the region (Nielsen, 1974; Brander, 2010). The combined effect of gradual water warming (Doney *et al.*, 2012) and the rising frequency of MHWs could therefore exert significant ecological pressure on this historically heavily exploited population, affecting both its survival and long-term resilience.

In the face of these environmental and socio-economic challenges, there is an urgent need to better understand how thermal variability, in particular rising temperatures and MHWs activity, affects the life cycle of whelks and the sustainability of the WEC fishery. The implementation of effective management strategies adapted to a changing climate is an increasing priority.

This is the context for the CCLIMB-UP project (Changement CLImatique en Manche : les effets sur le BUlot et son exPloitation). The main hypothesis is that climate change is altering temperature dynamics in the English Channel through both long-term warming trend and increased MHWs frequency, which affects the productivity of whelk stocks in the WEC and EEC, and therefore has an impact on the fisheries that depend on them. The objectives of this project are:

- To identify how temperature has changed over space and time in whelk habitats over the past decades.
- To explore how temperature affects key processes, focusing on growth and reproduction, using field studies and controlled experiments.
- To assess the sustainability of whelk stocks in the context of climate change and the fisheries that rely on them.

My Master's 2 internship aligns with axes 1 and 2 of this project, which, respectively examine the effects of changing environmental conditions on whelk biology in the English Channel, and then whelk stock dynamics, with the aim of assessing stock health and fishery sustainability.

During this internship, two main hypotheses were explored to better understand the links between seasonal temperature variability and whelk stock dynamics in WEC.
The first hypothesis is that high summer surface temperatures in WEC, especially when combined with MHWs may induce thermal stress in individuals. This stress could lead to higher mortality rates and, in turn, a short-term decrease in stock abundance.
The second hypothesis looks at the delayed effects of winter conditions in WEC on recruitment. Unusually warm winter, particularly if MHWs also occur, could disrupt key biological processes related to reproduction, reducing recruitment success. These disruptions could result in a decline in stock abundance observed three to five years later.

This task is particularly challenging because whelk is classified as a data-limited stock (DLS) (Hegron-Mace *et al.*, 2017). These stocks are characterised by a lack of data on abundance and population dynamics, making traditional fisheries assessment models ineffective (Cope, 2024). However, as Cope (2024) points out, "we have to do something better than nothing".
For DLS, a number of specific assessment models have been developed (Cope, 2024). These approaches need to be identified, compared and adapted to the data available for the WEC whelk stock. The aim is to propose relevant assessment methods that can be used to inform effective management measures, to ensure the long-term viability of this resource.

This master's thesis focuses on five key analytical components:

1. Characterization of the whelk fishery in the Western English Channel (WEC).
2. Analysis of seasonal and interannual thermal variability in the WEC and whelk habitats, including the detection and quantification of marine heatwaves (MHWs) in terms of average intensity, maximum intensity, frequency, and duration.
3. Development of a standardized landing-per-unit-effort (LPUE) index using declarative data on landings and fishing activity. This index will serve as a proxy for whelk abundance, supporting analyses of population dynamics and stock assessment.
4. Investigation of the relationship between long-term seasonal thermal trends, extreme events, and interannual variations in abundance using the constructed LPUE index.
5. Review of stock assessment methods suitable for data-limited (DLS) stocks, with a focus on approaches compatible with the available WEC whelk data. Selected methods are tested and compared, and, where appropriate, environmental variables identified earlier are incorporated into the models. The objective is to contribute to the development of a robust methodological framework that can support targeted and effective management measures to ensure the long-term sustainability of the stock.

This integrated approach, combining environmental, fisheries and biological data, aims to improve our understanding of the climate-related pressures on whelk population dynamics and provide concrete insights to improve the sustainable management of this resource.

2. Materials and methods

2.1. Life cycle of the common whelk (*Buccinum undatum*)

The whelk is a gonochorous benthic species whose life cycle is closely linked to the thermal conditions of its habitat (Kideys *et al.*, 1993). Reproduction begins in autumn (October-November), when water temperatures start to decline, and spawning occurs in winter, between December and January (Kideys *et al.*, 1993). Females lay between 500 and 2,000 eggs per capsule, although hatchability remains low (around 1%) (Smith and Thatje, 2013). Larger females generally produce more eggs, highlighting the importance of body size for reproductive output (Valentinsson, 2002).

They hatch between April and early May, after 3 to 5 months of intracapsular development. Unlike other molluscs, the whelk does not have a pelagic larval stage: juveniles develop within the capsule and feed on eggs (adelphophagy), which increases their probability of survival but makes them highly dependent on favourable benthic local conditions (Smith and Thatje, 2013).
Common whelks grow relatively rapidly during the first few years of life. Sexual maturity is generally reached between 3 and 4 years of age, with a mature size (L_{50}) estimated at 53 mm in the western Cotentin (Heude-Berthelin *et al.*, 2011). Latitude has a positive effect on size at maturity: whelks living at higher latitudes generally reach maturity later than those at lower latitudes, suggesting an effect of temperature on this biological parameter (Haig *et al.*, 2015). Other studies have shown a similar effect on the asymptotic size ($L\infty$) of populations (Emmerson *et al.*, 2020).

The whelk is a eurythermal species, able to tolerate temperatures ranging from 0 and 22°C (Kideys *et al.*, 1993). However, it remains sensitive to rapid thermal variations, which can disrupt its growth, reproduction or distribution (Smith *et al.,* 2013). A temperature threshold of around 9-10°C has been estimated to trigger reproduction (Kideys *et al.*, 1993). In summer, high temperatures (around 18 °C) can induce a “biological pause”, marked by reduced activity and feeding, increased mortality and reduced catchability (Nielsen, 1974). Fishermen report that whelks bury themselves in the sediment in search of a thermal refuge, although this observation, frequently reported, lacks empirical verification.

2.2 Study Area

The study area is the southern part of the WEC, with a focus on the Normandy-Brittany Gulf, which is the historical fishing ground for the WEC whelk stock (Figure 1). This geographic area is defined by the northern coast of Brittany and the western part of the Cotentin Peninsula (Santarelli Chaurand, 1985). The hydrological dynamics are dominated by strong tidal currents that constantly mix the water column. This intense vertical mixing prevents the formation of a stable thermocline and significantly limits the amplitude of seasonal variations in surface and bottom temperatures (Santarelli Chaurand, 1985). The Gulf of Normandy-Brittany is very heterogeneous in terms of sediments (Figure 1). The seabed consists of a diverse mix of substrates, including sand, fine sand, silt, mud, gravel, pebbles and rocky outcrops (Figure 1). This complex distribution is the result of the intense hydrodynamic dynamics of the area.

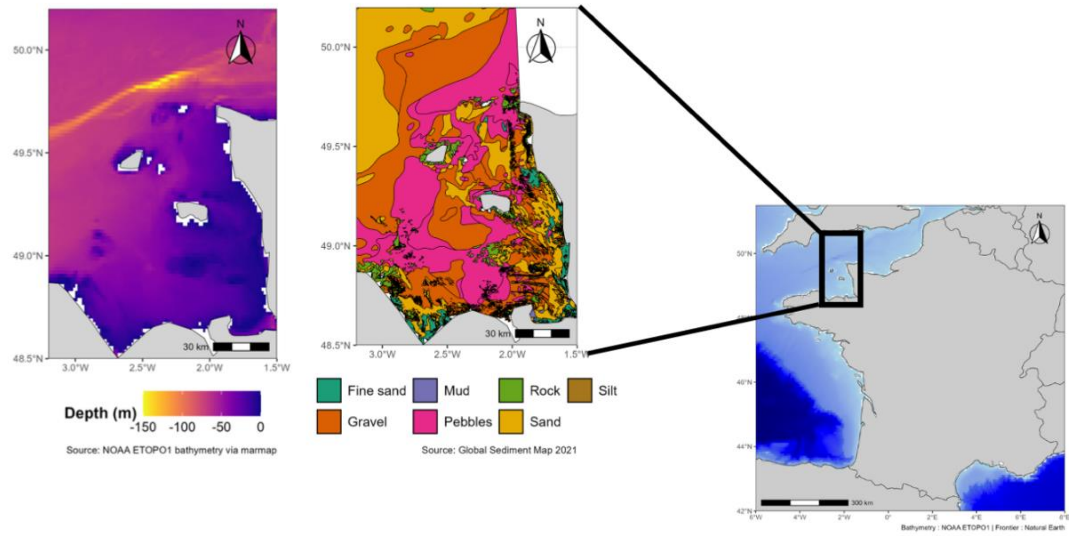

Figure 1. *Bathymetric and sedimentological characteristics of the Gulf of Normandy-Brittany (NOAA ETOPO1, 2025; Global Sediment Map, 2021).*

2.3. Whelk habitat proxy in the WEC

To investigate the spatial distribution of whelk habitats in the WEC, we use fishing activity as a proxy. By analysing vessel trajectories, we aim to infer areas of ecological relevance based on targeted whelk fishing grounds.

<u>2.3.1. Vessel tracking data</u>

This study is based on two main sources of vessel tracking data used to characterise the spatial and temporal activity of fleets targeting whelk in the WEC: the Vessel Monitoring System (VMS) and the Automatic Identification System (AIS). These systems were used to reconstruct vessel trajectories to provide a detailed representation of whelk fishing areas.

2.3.1.1 VMS data

Since 2010, European fishing vessels over 12 meters long are required by EU regulations to be equipped with a Vessel Monitoring System (VMS) (Council Regulation (EC) No 1224/2009). In France, data from these vessels are collected and stored by Ifremer’s Fisheries Information System (Système d’Information Halieutique, SIH), under the responsibility of the Directorate of Maritime Fisheries and Aquaculture (DPMA). The VMS data include the date, time, and location of vessels, recorded every hour. Ifremer uses this information to estimate fishing effort. While fishing activity was previously identified using a speed threshold (with vessels considered to be fishing if their average speed was below 4.5 knots), the current approach relies on an algorithm that detects distinct speed distributions rather than a fixed cutoff.

The VMS data used in this study cover the period 2001-2022. They include 86 vessels that reported at least one VMS position and landed whelk in the WEC, out of a total of 363 vessels targeting this species between 2001 and 2022. Although the frequency of positioning is lower than for AIS, VMS covers a larger number of vessels. Over the period, these data represent 6.46% of whelk landings, mainly concentrated at the end of the time series.

2.3.1.2 AIS data

The Automatic Identification System (AIS), introduced by the International Maritime Organisation (IMO), enhances maritime safety and prevents ship collisions (IMO, 1974). This system system automatically broadcasts vessel position, course and speed at high frequency (generally every 2 to 5 minutes) via FM radio. In France, AIS has been mandatory since 2019 for vessels over 15m in length and for certain vessels between 10 and 15m operating in densely trafficked maritime areas. These data are provided by CEREMA (Center for studies and expertise on risks, the environment, mobility and planning).

The AIS data used cover the period 2016-2023 and include 33 vessels targeting whelk in the WEC, out of the 194 vessels operating in the area during this period. They represent 4.5% of whelk landings over this period. These data cover a small number of vessels but provide a high resolution of their trajectories.

2.3.2. Data processing and filtering

The VMS and AIS datasets were pre-processed by Anna Mazaleyrat (postdoctoral researcher at Ifremer, Port-en-Bessin). This pre-processing involved removing inconsistent data points, such as positions on land or unrealistically high speeds. After cleaning, the data were converted to parquet format to make processing easier.

The datasets were then combined using information from the SACROIS database (Système d'Acquisition et de CROisement d'Informations Statistiques), an algorithm that merges several data sources, including landing declarations, to identify fishing activity by species. This allowed us to isolate the vessels that had landed whelks in the WEC.

2.3.2.1. Calculation of speed and assignment of status

For both datasets, vessel speeds targeting whelks were recalculated to correct inconsistencies that persisted despite pre-processing in the initial speeds derived from VMS and AIS data, thereby ensuring data quality. Speed was recalculated as the ratio of the geographical distance between two consecutive GPS points to the time elapsed, converted to knots. A status was assigned to each point: points associated with a speed ≤ 3 knots were considered to correspond to fishing activity (trap hauling), those with a speed > 3 knots were considered to be in transit.

For the VMS data, a double filter was applied: the first based on the status declared by the fisherman (fishing), and the second based on the recalculated speed. Only points meeting both criteria were retained as representative of the whelk fishery. For the AIS data, which include a non-mandatory declared status, the filter was based on speed only.

2.3.2.2. Temporal filtering

Vessels fishing whelks with pots often hold multiple licenses and target different species throughout the year, mainly crustaceans and cuttlefish. Therefore, during a fishing trip, they do not focus solely on whelks. To isolate the specific whelk fishing activity, a time filter was applied: only the months corresponding to the peak whelk fishing season, identified from landing data in the SACROIS database, were kept. This period covers February to June.

Integrating VMS and AIS data, combined with temporal and behavioural filters, facilitates the identification of whelk fishing areas in the WEC, despite the partial coverage of the fleet. This method provides a proxy for whelk habitat. While each year was analysed individually (Appendix. 4 and 5), results were aggregated due to the absence of significant shifts in fishing ground over the considered period.

2.4. Characterizing whelk fisheries in the WEC

This section presents the historical dynamics of whelk fisheries in WEC, with a focus on trends in landings and fishing effort over time. Data from multiple sources, including French and Jersey fisheries statistics, were compiled and analysed to provide a broad and consistent overview of the fishery from 1973 to 2024.

2.4.1. Historical catch from 1973 to 2024

Data were compiled from national French databases (including 'Maritime fisheries statistics' database, the Normandy Regional Marine Fisheries Committee and SACROIS) and from the Government of Jersey's official landing statistics. These complementary sources help document the evolution of whelk landings over the past five decades, and provide context for understanding current trends in the WEC fishery.

2.4.1.1. The SACROIS database - Landing data between 2000 and 2024

The data used in this study come mainly from the SACROIS database (Système d'Acquisition et de CROisement d'Informations Statistiques), developed and managed by IFREMER. This database centralises information on professional fishing activities in France from administrative, scientific and reporting sources. It aims to provide consolidated, qualified and consistent data on the activity of fishing vessels registered in the Community Fishing Fleet File (FPC) (Demaneche *et al.*, 2023).
SACROIS is based on the collection and cross-referencing of several, sometimes conflicting, data sources to produce reference information. The main sources used include fishing logbooks declared by vessel owners and skippers, auction sales data, wholesale receipts and vessel monitoring system (VMS) data (Demaneche *et al.*, 2023). This information is supplemented by direct observations and trade surveys carried out by IFREMER. Thanks to a matching and validation algorithm, SACROIS does not directly correct the data, but selects the best available information to provide a consolidated and reliable summary (Demaneche *et al.*, 2023).
The SACROIS database (2000-2024) was used as the main source for French whelk landings in the WEC. Several filtering and correction steps were applied to ensure data quality, including reallocation of misreported landings between WEC and EEC and removal of aberrant values. A detailed description of these procedures is provided in Appendix 6.

2.4.1.2. Historical landing data - period 1973-1999

Before the SACROIS database existed, historical whelk landings in the WEC were reconstructed by aggregating data from multiple sources. French landings between 1973 and 1999 were integrated from the 'Maritime fisheries statistics' database for the period 1973-1983, covering the maritime districts of Cherbourg, Saint-Malo and Saint-Brieuc. For the period 1984-1999, the data come from the Normandy Regional Marine Fisheries Committee, with data provided by Marie-Laure Cochard as part of the Bestclim project (Hegron-mace *et al.*, 2017).

2.4.1.3. Landing data from Jersey - period 1997-2022

Whelk landing data for Jersey between 1997 and 2022 were compiled from two sources: Morel and

Bossy (2004) for the years 1997-2001, and official online statistics for 2002-2022. Some inconsistencies were detected in the reports for the years 2000, suggesting possible retrospective corrections.

2.4.2. Variations of the fishery landing whelk over space and time

During the SACROIS period, from 2000 to 2024, the number of vessels, total landings, and annual fishing trips were quantified to assess temporal and spatial fishing dynamics. Particular attention was paid to spatial landing data by ICES statistical rectangles to highlight geographic variation. Vessel characteristics, such as average size and engine power, were also tracked annually to better understand the evolving profile of the whelk fishing fleet.
For the earlier period, prior to the year 2000, the analysis focused exclusively on the time series of French whelk landings in the WEC.

2.5. LPUE indices from French fleets

2.5.1. Rationale for using LPUE as an indicator of whelk abundance

Estimates of whelk abundance in the WEC area are based on several indicators, notably landings per unit of effort (LPUE). This method is widely used in fisheries science to estimate the relative abundance of an exploited population by assuming a relationship between reported landings relative to effort and stock density (Maunder and Punt, 2004). It is particularly relevant in cases where no dedicated scientific survey is conducted, which prevents the estimation of abundance indices from standardized, fisheries-independent survey. The analysis of changes in LPUE over time makes it possible to detect potential signs of stock decline and adjust management accordingly.
As shown in the work of Mauder and Punt (2004), the relationship between catch/landing rate (CPUE, or LPUE in the case of landings data) and stock abundance is described by the equation:

$$L_t = q*E_t*D_t - R_t \qquad \text{or} \qquad C_t = q*E_t*D_t$$

where E is the fishing effort, D is the average density of the exploited stock, q is the catchability coefficient (which depends on the efficiency of the fishing gear), and R represents the discards The subscript *t* denotes the relation for year *t*. It follows from this relationship that:

$$LPUE_t = L_t/E_t = q*D_t - R_t/E_t \qquad \text{or} \qquad CPUE_t = C_t/E_t = q*D_t$$

2.5.2. Landing and effort data

LPUE was calculated from catch data in the SACROIS database (trip level). To ensure consistency and limit bias, a reference fleet was established. This fleet corresponds to a subset of vessels showing coherent activity in terms of gear use, fishing area, temporal coverage, and regularity over time, and was defined by applying several filters related to gear, fishing area, seasonality, activity regularity, crew size, and outlier values (see detailed description in Appendix 7). Fishing effort is reported in SACROIS through vessel activity, but this information is not consistent for pot fisheries. Therefore, effort was approximated using crew size derived from the SIH vessel activity calendar. After filtering and merging effort with catch data, 29.3% of the initial landings were retained for LPUE estimation, corresponding to 95,494 trips out of an initial 334,229.

2.5.3. Standardisation of LPUE through Generalized Additive Modelling (GAM)

LPUE is used as an index of abundance but must be interpreted with caution, as whelk availability depends on environmental conditions (e.g., temperature, seabed type) and catchability varies with gear efficiency and fishing strategies. To reduce these biases, LPUE was standardized to separate structural effects from abundance trends (Maunder and Punt, 2004). Standardization focused on two major sources of variability: seasonality (month) and inter-vessel differences.

The model was fitted using a Generalized Additive Model (GAM, mgcv package in R; Wood, 2017), which can capture potential non-linear relationships (Venables and Dichmont, 2004). However, no non-linear effects were detected, so the final model corresponds to a Generalized Linear Mixed Model (GLMM), including a random vessel effect to account for inter-vessel variability and avoid biases linked to performance or fishing strategy. Fishing effort was included as an offset to standardize landings, ensuring correct estimation of covariate effects on abundance. A logarithmic transformation of landings was applied to stabilize variance and reduce the influence of extreme values. Year was included as a covariate to extract the underlying temporal trend independently of seasonal and vessel effects.

Several probability distributions (lognormal, gamma, Tweedie) were tested, and the model fit was evaluated using the Akaike Information Criterion (AIC) (Appendix. 8). Residual and variance diagnostics confirmed the robustness of the fit (Appendix. 9). Based on the selected model, an annual abundance index was constructed by generating predictions under standardized conditions (constant effort, mean vessel effect, inclusion of all months). Predictions were made on the log scale and back-transformed to the natural scale using the exponential function, with Laurent's correction applied to limit transformation bias (Appendix. 10).

Monthly predictions were then aggregated by year to produce a time series of annual LPUE indices, accompanied by confidence intervals. In parallel, raw LPUE values were obtained by simple annual averaging of observations. Comparing standardized and raw LPUE values allows assessment of how the model influences the detection of temporal trends by isolating the effects of fishing effort, seasonality, and vessel identity.

2.6. Analysis of SST and MHWs in the WEC

To assess the potential influence of temperature on the dynamics of the whelk, we first examined trends in sea surface temperature (SST) and MHWs across the entire WEC, and then more specifically within the estimated habitat of the whelk in the WEC (see Section 2.3). The analysis is based on surface temperatures, as reliable and homogeneous bottom temperature data are scarce in this region. Given the shallow depth of the WEC and the significant vertical mixing, it is reasonable to assume that surface thermal dynamics are representative of, or at least correlated with, those observed at depth (see section 2.2).
Surface temperature therefore constitutes an accessible and relevant indicator for evaluating thermal constraints that may affect benthic species such as the whelk. The aim here is to identify long-term thermal trends as well as seasonal anomalies that could influence the species' physiology, behaviour, or distribution.

Summer is defined as the period from July to September, with June excluded due to generally moderate temperatures. This temporal framework is based on ecophysiological considerations: ocean heat accumulation typically peaks in September (Agoumi, 1982). Including July, August, and September thus better captures the potential impact of the year's most extreme heat events. Other seasons were defined consistently to allow comparisons throughout the annual cycle.

2.6.1. Temperature data

The sea surface temperature (SST) data used in this study come from the OISST database developed by NOAA (Reynolds *et al.*, 2007). Version 2 provides daily estimates since 1982 at a 0.25° (~25 km) resolution. OISST combines multiple sources through optimum interpolation to ensure consistency and reduce errors: infrared satellite data (AVHRR), limited by cloud cover; microwave data (AMSR-E, AMSR2, WindSat), which penetrate clouds but are less reliable near coasts; and in situ observations from buoys and ships, used to correct satellite biases (Reynolds *et al.*, 2007). Climatology and modelling are applied to fill gaps, while a 7-day temporal smoothing reduces noise and highlights background trends. This methodology makes OISST a reference for monitoring ocean warming, detecting marine heatwaves (MHWs), and assessing the impacts of temperature variability on marine ecosystems (Reynolds *et al.*, 2007; Smale *et al.*, 2019; Simon *et al.*, 2023)

2.6.2. SST data processing

OISST data between 1983 and 2024 were downloaded from the NOAA server (https://downloads.psl.noaa.gov//Datasets/noaa.oisst.v2.highres/sst.day.mean.nc) to analyse daily thermal variations in the WEC (Reynolds *et al.*, 2007).
The first step was to select data covering ICES fishing area 7e, which corresponds to the WEC, based on the coordinates defined for the French whelk fishery. The analysis focused on ICES statistical subdivisions 26E7, 26E8 and 27E8 (Figure 2), which were identified from VMS, AIS and SACROIS data as being linked to the estimation of whelk habitat.

The analysis steps included calculating seasonal and annual averages of SST to observe long-term thermal trends. In addition, monthly averages were computed for three reference periods (1983-1988, 2000-2004, and 2019-2024) in order to highlight potential shifts in seasonal thermal regimes over time and to better capture changes in the intensity and timing of warming across decades.
For each analysis of the annual and seasonal averages examined over time, two types of models were fitted and compared: a simple linear model and a second-degree polynomial model. Based on the analysis of residuals and the AIC criterion (Appendix. 11 and 12), the simple linear model was preferred. These models aimed to determine whether there was a significant increase in temperature, both annually and seasonally, and to identify which seasons showed the steepest slopes, indicating the most pronounced warming.

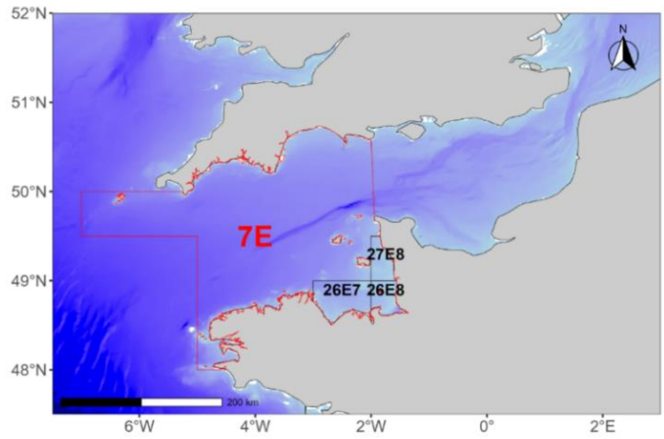

Figure 2. *ICES whelk fishing area in the WEC and and the spatial extent of the ICES division 7E (WEC).*

<u>2.6.3. Detection and characterization of MHWs</u>

2.6.3.1. Detrending data

The long-term temperature trend in SST was removed prior to the detection of MHWs (MHWs), in order to more effectively isolate short-term extreme anomalies from gradual ocean warming. This approach is based on several recommendations from the literature (Laufkötter *et al.*, 2020; Xu *et al.*, 2022), which emphasize the importance of clearly distinguishing between these two distinct thermal phenomena. Following the shifting baseline definition, MHWs are understood as transient, extremely warm temperature events that are anomalous relative to the expected conditions for a given location and time, based on a recent and evolving climatological reference period (Amaya *et al.*, 2023).
Removing the long-term trend helps avoid collinearity between mean SST and MHW metrics, which could otherwise bias the interpretation of their respective impacts (Hobday *et al.*, 2016; Smale *et al.*, 2019). Indeed, while long-term warming may increase the statistical likelihood of MHW occurrence, this does not necessarily imply that such events are truly more frequent or intense (Laufkötter *et al.*, 2020). This methodological choice allows for a clearer separation between the acute, short-lived impacts of MHWs and the chronic, progressive effects of long-term warming, in line with the proposed framework for assessing total heat exposure, that is, the combined influence of both long-term temperature trends and extreme thermal events on marine ecosystems (Amaya *et al.*, 2023).

Daily SST data were detrended over the period 2000-2024 prior to MHW detection. A relatively short baseline period was chosen (shorter than the conventional 30-year climatology), thereby enhancing the ability to detect recent anomalies and ensuring consistency when linking thermal extremes to potential ecological responses. This also reduces potential biases associated with longer climatology, which can obscure recent shifts in oceanographic regimes (Farchadi *et al.*, 2025).
The 2000-2024 reference period was also selected to match the temporal coverage of LPUE, making it a suitable compromise between a short climatological window and the need to assess the potential impact of thermal events on species abundance.

2.6.3.2. MHW detection

For the entire study area, the daily SST time series were first fitted using the model that best captured seasonal and interannual variability (see Appendix 13 for model selection details).

The residuals from this fit were then used to detect MHWs, by applying a moving threshold defined as the 90th percentile of the residual distribution. Following Hobday et al. (2016), a marine heatwave is defined as at least five consecutive days above this threshold, a criterion chosen to exclude short spikes detection was performed using the R package *heatwaveR* (Schlegel and Smit, 2018). Events were characterized based on several metrics: annual and seasonal mean intensity, annual and seasonal cumulative duration, and annual and seasonal mean maximum intensity.

2.7. Thermal stress thresholds and summer impacts on whelk stock dynamics

To investigate the potential influence of temperature on stock abundance, two complementary approaches were implemented. Although methodologically distinct, they share the same overarching objective: understanding how long-term warming and MHWs might affect the exploited whelk population.

The first approach (Section 2.7.1) is exploratory and qualitative. It draws on the literature to identify biologically relevant thermal thresholds for whelks, applied separately to winter and summer temperature conditions.

The second approach (Section 2.7.2) is based on a statistical analysis focused on summer conditions. This method aims to quantify the potential effect of mean summer temperature and the occurrence of MHWs on the stock, using generalized additive models (GAMs).

2.7.1. Qualitative biological approach

As a first approach, the study relied on the literature to identify relevant biological thresholds for whelk. For winter, a threshold of 9.5 °C was selected, corresponding to the temperature range (9 to 10 °C) at which spawning is triggered in this species (Kideys *et al.*, 1993). For summer, a threshold of 18 °C was used, which is the temperature above which whelks cease all activity (Nielsen, 1974). The OISST data, available at daily resolution, were used to calculate the percentage of summer and winter days during which SST was above or below these biological thresholds, in order to assess the evolution of potential thermal stress experienced by the species in its habitat.

2.7.2. Quantitative statistical approach

In parallel, the second approach is based on a statistical analysis focused on summer conditions, under the hypothesis that high summer temperatures and the occurrence of MHWs directly increase mortality in the species. Mean summer temperatures and the presence of MHWs were lagged by one year to account for the fact that LPUE is calculated over the period from February to June (see section 2.5.2). This allowed for testing the potential delayed effect of summer environmental conditions on the exploited stock. The mortality induced in year n is therefore expected to be reflected in the abundance observed in year n+1. The data used for this analysis included time series of LPUE between 2000 and 2024 (see section 2.5), mean summer temperatures (see section 2.6.2), and binary variables indicating the presence of summer MHWs (see Section 2.6.3.2).

$$\log(E[Y_t]) = \beta 0 + \beta 1 * MHW_{t-1} + f(temp\_summer_{t-1}),\ Y_t \sim N(\mu_t, \sigma^2) \qquad \text{Eq. 1}$$

where:

- **$\log(E[Y_t])$** = Logarithm of the expected LPUE in year t; this is the response modelled in the GAM with a log link function, ensuring positivity of the predictions.
- **β0** = Intercept term, representing the baseline log-mean LPUE when no MHW is present and temperature is at the reference level.
- **$\beta1 * MHW_{t-1}$** = Linear effect of the presence of a marine heatwave (MHW) during the previous summer (year t−1); MHW is a binary variable (0 = absent, 1 = present).
- **$f(temp\_summer_{t-1})$** = Smooth function capturing the potentially nonlinear effect of mean summer temperature in year t−1.
- **$Yt \sim N(\mu_t, \sigma^2)$** = Assumes that LPUE follows a normal distribution (N) with mean μ_t and constant variance σ^2.

A series of GAM models were tested to quantify the effect of summer temperature (in year n-1) and the presence of a MHW (in year n-1) on stock abundance (in year n). One example of these models uses a Gaussian distribution, where the logarithm of the expected LPUE value is modelled as a function of temperature and the presence of a MHW (see Eq. 1). Other model configurations using different probability distributions (Gamma, Tweedie) were also tested and are presented in Appendix 29.
These models were compared using the Akaike Information Criterion (AIC) to identify the most parsimonious model. The normality of the residuals was assessed using the Shapiro-Wilk test, supplemented by visual inspection of theoretical quantiles (Q-Q plot) (Appendix. 15). The homogeneity of variance was also checked using residuals versus fitted plots to ensure consistency across the range of fitted values.

2.8. Stock assessment

Full analytical stock assessments (SS3 or VPA) are not possible for whelk in the Western English Channel due to major data limitations: biological sampling is both limited and inconsistent over time, and key life-history parameters, such as growth, maturity, or natural mortality remain highly uncertain or unknown. This prevents robust estimation of parameters in integrated models. In the absence of reliable data, the assumptions required for analytical models would be too strong, leading to unreliable results. Therefore, adapted methods are essential alternatives to support management in such data-limited contexts.

2.8.1. Biological database

As part of several research projects conducted between 2009 and 2025, including Gestion durable des pêcheries, BULOCLIM, BESTCLIM, ESHANO, MECANOR, COGECO and CCLIMB UP, whelks were sampled in the WEC during targeted sampling campaigns. These campaigns were carried out by various stakeholders, including the SMEL (Syndicat Mixte Mer-Littoral), the CRPMEM (Comité Régional des Pêches et des Elevages Marins) of Normandy and IFREMER. Data collection campaigns did not take place in certain years during this period, specifically 2010, 2012, 2014, 2016, 2020 and 2024. In years where data was available, the number of individuals measured generally ranged between 9,000 and 18,500. Notable exceptions occurred in 2017 and 2019, when only 2,948 and 1,832 individuals were sampled respectively due to reduced sampling effort.

Sampling campaigns were conducted aboard commercial whelk fishing vessels using baited pots as

fishing gear. To maximise the representativeness of the size structure of the exploited stock, size-sorting grids, which are typically used in commercial fishing, were not applied. This approach allowed all size classes to be retained in the sample.
Despite some variations in sampling protocols between projects, biometric data were standardised to ensure comparability. A total of 122,013 individuals were measured to determine the height of their shells, 74,936 were weighed with their shells, and 61,767 were measured to determine the width of their shells.

2.8.2. Biological data requirement

The selectivity estimates enable the size composition of individuals retained or discarded by the sorting grid[1] to be reconstructed using a dataset. This allows fishing gear selectivity to be integrated into subsequent analyses, particularly for estimating:

- The exploited size distributions.
- The modal size of the catch, as well as the length at first capture (Lc).

This approach supports the DLS (Data-Limited Stock Assessment) methods developed by ICES, which rely on the size structure of the commercially retained fraction. By reconstructing this fraction based on gear selectivity, these methods can be applied even in the absence of size data from landings, since catches are sorted directly on board.
From 2021 to 2025, selectivity measurements were conducted aboard commercial vessels targeting whelk in the WEC, using a regulatory sorting grid with 22 mm mesh size. During these surveys, all individuals captured regardless of size were systematically tested against the grid. For each individual, it was recorded whether it passed through the grid (rejected fraction) or was retained above it (retained fraction). Each specimen was measured for shell height (mm) and classified according to its position relative to the grid.
These data were used to model the probability of retention as a function of shell height using a logistic regression model (binomial distribution) (Millar, 1992). The model was fitted using the glm() function in R (Myers *et al.*, 2012), specifying the binary response variable (retained/rejected) and shell height as the explanatory variable. The model takes the following form:

$$\text{logit}(pi)=a*Hi + b \qquad \text{Eq. 2}$$

where:

- pi is the probability that individual is retained,
- Hi is the height of the individual i (in mm),
- b is the intercept
- a is the slope coefficient associated with Hi

From these coefficients, the characteristic points of the selectivity curve are derived:

- SL_{50} (size at 50% retention probability): $SL_{50} = -\alpha/\beta$

[1] The sorting of caught individuals must be carried out on board vessels in French waters using a grid that separates individuals based on their width. For individuals measuring 45 mm in height, the estimated width is 20.3 mm. To ensure compliance with the minimum legal size, the spacing between the grid bars is set at 22 mm (Guide des espèces,2024)

- SL_{95} (size at 95% retention probability): $SL_{95} = (\log(0{,}95/(1-0{,}95)) - \alpha)/\beta$

The logistic curve is fitted using the predict() function applied to a sequence of sizes. In order to quantify the size structure of individuals actually retained or rejected by the sorting grid used in commercial fishing, the estimated selectivity function (see previous section) is applied to all collected biological data.

For this, each individual observation is assigned a retention probability (pi) based on its size, obtained from the logistic selectivity model (Eq.2). This probability is averaged by size class (rounded down to the nearest millimetre) to ensure consistency between the model resolution and that of the observations. Individuals are probabilistically split according to their potential status relative to the sorting grid:

- A fraction is considered retained with a weight equal to pi,
- A fraction is considered discarded with a weight equal to 1 − pi.

2.8.3. Stock assessment status

Two approaches, LBI and SPiCT, were chosen because they are well suited to data-limited situations, allowing useful diagnostics even with incomplete information. They are complementary: LBI, based on commercial size distributions obtained from whelks sampled across various projects and adjusted for gear selectivity, quickly provides indicators of relative status (fishing pressure, biomass) using simple ratios (Lmax5%, Pmega, Lmean…) to assess sustainability. SPiCT, on the other hand, uses time series of catches (SACROIS) and abundance indices (LPUE) calculated to model biomass dynamics over time, providing estimates of absolute and relative biomass, productivity, and associated uncertainty. Together, these approaches allow cross-validation of information to strengthen the diagnosis, explore different stock dimensions, and test the coherence of results, fitting into a progressive framework of increasing model complexity recommended for managing stocks under data-limited conditions.

2.8.3.1. Length-Based Indicator (LBI)

2.8.3.1.1. Method description

In this context, the Length-Based Indicators (LBI) recommended by ICES (2018) provide a standardized framework for assessing stock status based on the size composition of landings. The ICES technical guidelines present key indicators (Lmean, Lmax5%, Lc, L95%) along with their reference ratios, which allow the evaluation of aspects related to conservation, yield optimization, and exploitation at maximum sustainable yield (MSY) levels (Table 1).

2.8.3.1.2. Asymptotic length (L_∞)

To parameterize these indicators, the asymptotic length (L_∞ or Linf) used in this analysis comes from the BESTCLIM project, where it was estimated from a limited dataset (n = 39 individuals), leading to considerable uncertainty. This uncertainty is accounted for in the analysis by incorporating the lower and upper bounds of L_∞, as recommended by ICES (2018).

2.8.3.1.3. Optimal length (L_{opt})

The optimal length (L_{opt}), which corresponds to the ideal size to maximize yield per recruit, is defined as the length at the inflection point of the von Bertalanffy growth curve, that is the point beyond which individuals stop growing rapidly and the energy invested in somatic growth decreases significantly. Lopt is calculated using the relationship $L_{opt} = 2/3 \times L\infty$. The proxy $L_{F=M}$, which represents the length at which fishing mortality (F) equals natural mortality (M), is estimated using the formula $L_{F=M} = 0.75 \times Lc + 0.25 \times L\infty$, assuming a M/K ratio of 1.5, as proposed by ICES (2018). This reference length serves as a proxy for maximum sustainable yield (MSY).

2.8.3.1.4. Maturity length (L_{mat})

Maturity length (L_{mat}), or the length at which 50% of the whelk population in the WEC is mature, was estimated at 50 mm in the BESTCLIM project and at 53 mm in the study by Heude-Berthelin *et al.* (2011). This uncertainty in maturity size will also be considered in the analyses.

Table 1. *Length-based indicators used for the assessment of data-limited stocks (status 3 and 4) (ICES, 2018).*

Indicator	Calculation	Reference point	Indicator ratio	Expected value	Property
$L_{max5\%}$	Mean length of largest 5%	L_{inf}	$L_{max5\%}/L_{inf}$	>0.8	Conservation (large individuals)
P_{mega}	Proportion of individuals above Lopt + 10% (L_{opt} is estimated from L_{inf})	0.3-0.4	Pmega	>0.3	Conservation (large individuals)
$L_{25\%}$	25th percentile of length distribution	L_{mat}	$L_{25\%}/L_{mat}$	>1	Conservation (immatures)
L_{mean}	Mean length of individuals > Lc	$L_{opt} = 2/3\ L_{inf}$	L_{mean}/L_{opt}	>1	Optimal yield
L_{mean}	Mean length of individuals > Lc	$L_{F=M} = 0.75Lc + 0.25\ L_{inf}$	$L_{mean}/\ L_{F=M}$	>1	MSY

2.8.3.2. Surplus Production in Continuous Time (SPiCT)

To assess the status of the whelk stock in the WEC in a context of limited data, we used the SPiCT (Stochastic Production model in Continuous Time) model (Pedersen and Berg, 2017). SPiCT is a stochastic continuous-time surplus production model that allows the growth of exploitable biomass to be represented while explicitly incorporating process and observation errors (Pedersen and Berg, 2017). The model follows a complete state space structure, in which stock biomass (B_t) and instantaneous fishing mortality (F_t) are modelled as latent processes, estimated from time series of commercial catches (C_t) (from SACROIS, for example) and abundance indices such as LPUE (I_t). Biomass dynamics are expressed by a stochastic differential equation:

$$dB_t = m\,[(B_t/K) - (B_t/K)^n]\,dt - F_tB_tdt + \sigma_B B_t dW_t \qquad \text{Eq. 3}$$

where:

- *K* is the carrying capacity,
- *m* maximum sustainable yield (MSY),
- *n* the shape parameter of the production curve,
- σ_B the intensity of random variability (process error).
- W_t the Brownian motion.

SPiCT models the dynamics of fishing itself, allowing fishing mortality to be treated as a random process with its own variability (σF), with the possibility of incorporating seasonal patterns via cyclic splines or coupled stochastic differential equations (Eq. 3) (Pedersen and Berg, 2017).
SPiCT provides stock condition diagnostics as well as management benchmarks (which LBIs do not provide) in situations where traditional approaches (VPA, age-structured models) are not applicable.

The dataset includes 25 years of catch observations and 25 years of abundance indices (LPUE) between 2000 and 2024. The model was implemented in the R environment using the SPiCT library. The parameters were estimated by maximising the likelihood, with confidence intervals (95%) calculated using the Laplace approximation (Kristensen *et al.*, 2016). The model was solved numerically in continuous time with an integration step of 1/16 year (0.0625 years) using a Euler scheme.
Model adequacy and statistical assumptions were evaluated using OSA residual diagnostics (One-Step-Ahead residuals). Residual autocorrelation was tested with the ACF and Ljung-Box test, bias was assessed through prediction error trends, and normality was examined with the Shapiro-Wilk test and Q-Q plots. A sensitivity analysis with 10 random initializations confirmed numerical stability.
A retrospective analysis, progressively excluding the last four years, was used to evaluate stability of biomass and fishing mortality estimates. Mohn's rho was computed to quantify retrospective bias, with $|\rho| < 0.2$ considered acceptable (Hurtado-Ferro *et al.*, 2015).

A prior for the intrinsic growth rate (r) was specified as $\log(r) \sim N(\log(0.57), 0.32)$, constraining r to biologically plausible values (0.3-1.1). This choice reflects the available biological knowledge on whelks, a slow-growing benthic species, and allows extreme and implausible values to be excluded. It is also consistent with estimates reported in a Canadian study (Barrett, 2023) and in the SealifeBase database (www.Sealifebase.org), where r was estimated at about 0.57 for whelk. The shape parameter n was fixed at 2, following Schaefer's model formulation, commonly applied in data-limited situations to ensure identifiability and a symmetrical production curve (Schaefer, 1991).

3. Results

3.1. Characteristics of the fishery

Analysis of the density of VMS and AIS positions recorded by 119 vessels targeting whelks and operating in the WEC between 2012 and 2023 shows a high concentration of fishing activity in ICES statistical rectangles 26E8, 26E7, and 27E8, identified as the main whelk fishing areas (Figure 3A). This distribution highlights the relative spatial stability of fishing effort, concentrated to the south and west of the Cotentin Peninsula and to the east of the Bay of Saint-Brieuc (Figure 3A). In contrast, peripheral areas display a much lower density of points, probably reflecting lower fishing intensity or potentially lower resource availability. This is particularly evident in statistical rectangles 27E7, 28E7, and 28E8, where few or no VMS or AIS positions were recorded over the study period (Figure 3A). The spatial origin of whelk landings, aggregated at the ICES subarea level, confirms that most landings originate from rectangles 26E8, 26E7, and 27E8, with negligible contributions from adjacent subareas (Figure 3B). The statistical rectangles identified as the main fishing grounds will therefore serve as a proxy for the exploited whelk habitat, providing a geographical reference for subsequent analyses.

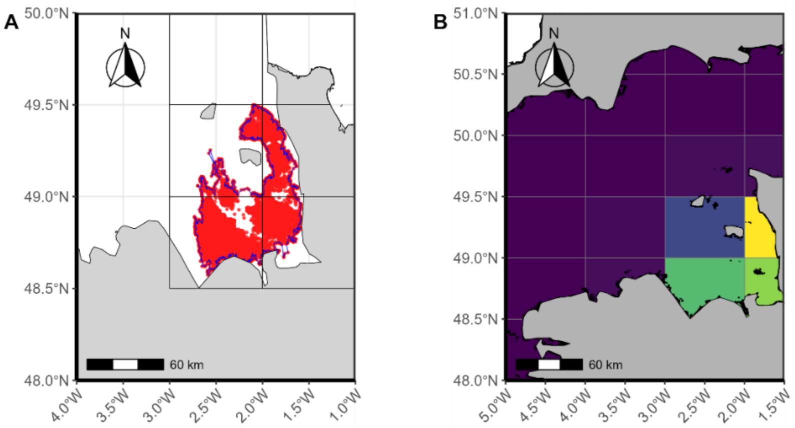

Figure 3. *Aggregated spatial distribution of VMS and AIS positions of whelk fishing vessels operating in the WEC between 2001 and 2023 (A) and ICES Subareas of origin for whelk landings, 2000 to 2024 (lighter squares = higher landings) (B).*

Landings of common whelk in the WEC show a sharply contrasting dynamic between 1973 and 2023 (Figure 4). Between 1973 and 1991, landings gradually increased from less than 2,500 tonnes to around 7,000 tonnes (Figure 4). This growth accelerated in the early 1990s, reaching a peak of around 14,000 tonnes in 2004, doubling production in 13 years (Figure 4). A downward trend began in 2005 (Figure 4). There was an initial decline between 2005 and 2011, followed by a period of relative stability, with landings fluctuating between 9,000 and 11,000 tonnes until 2017 (Figure 4). From 2018 onwards, landings fall sharply from over 10,000 tonnes to less than 3,000 tonnes in 2023, a reduction of almost 70% in six years (Figure 4).

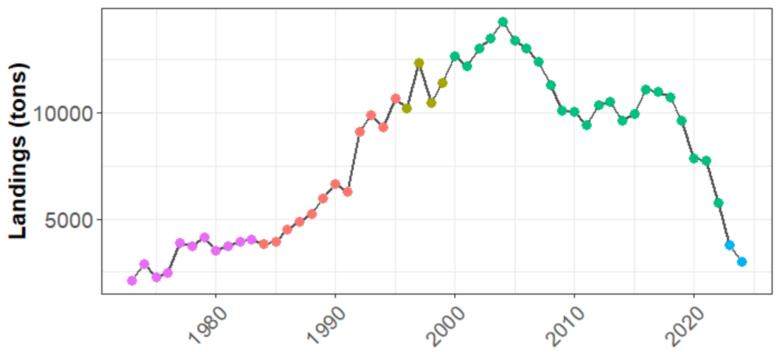

Figure 4. *Annual Landings of whelk in the WEC from 1974 to 2023 (Violet = Brittany and Normandy; Red = Normandy only; Marron = Normandy and Jersey; Green = Brittany, Normandy and Jersey (SACROIS data) ; Blue = Brittany, Normandy (SACROIS data)).*

Landings of common whelk show a marked seasonal variation, with recurring peaks and troughs over the months (Figure 5A). Catches of common whelk tend to peak between March and June. During this period, monthly landings often exceed 1,500 tonnes, with peaks of 2,000 tonnes in some years (Figure 5A).

The months from July to September show a decline in landings, with values often below 1,000 tons (Figure 5A). The months from October to February show a gradual recovery in catches, with volumes generally fluctuating between 500 and 1,500 tons (Figure 5A). This period indicates a recovery in fishing activity after the season of low catches, which also varies greatly from year to year (Figure 5A). There has been a dip in January since 2007, when the whelk fishing starting being closed during this month (Figure 5A). The seasonal nature of whelk catches is highlighted by large catches in spring and smaller catches in summer. A comparison between 2000-2006 and 2018-2024 reveals a shift in the monthly distribution of whelk catches (Figure 5B). From February to July, the share of annual catches increases in the recent period, while it declines from August to December (Figure 5B). These changes suggest a shift toward more seasonal fishing, likely reflecting adaptation to resource availability, especially in summer.

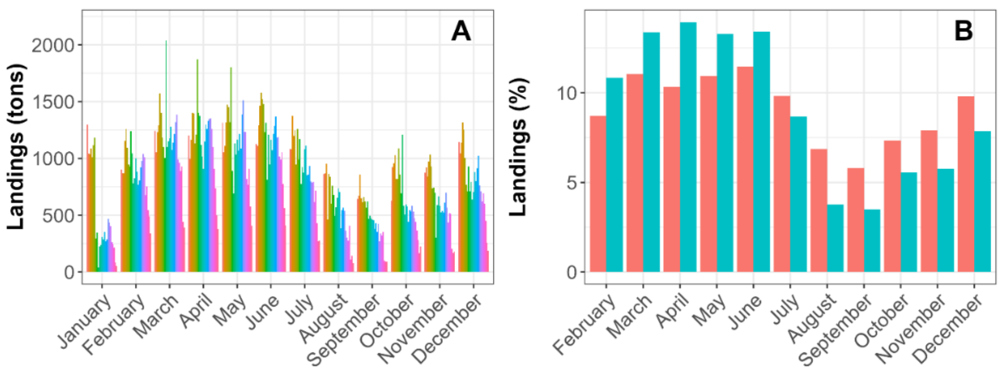

Figure 5. *Monthly landings of whelks in the WEC from 2000 to 2024, with each color representing a different year (A). Percentage of monthly landings of WEC whelks (excluding January due to fishery closure since 2007) for two periods, 2000–2006 (red) and 2018–2024 (blue) (B).*

Whelk fishing expanded in the early 2000s, with vessel numbers rising to 211 in 2007 (+16.6% vs. 2000) and trips peaking at 17,373 in 2006 (+94.7%) (Figures 6A, 6B and Appendix. 16). Fishing activity remained relatively stable until 2018, despite occasional declines such as n 2009 and 2012. Between

2018 and 2024, vessel numbers dropped from 187 to 103 (-44.9%) and trips from 16,275 to 8,213 (-49.5%), marking a clear reduction in fishing effort, possibly reflecting changes in resource abundance. The relationship between two proxies of fishing effort measured by the number of vessels and trips targeting whelks and annual landings over the period 2000-2024. The number of vessels shows a significant, positive correlation with total landings ($R^2 = 0.60$; $p < 0.001$) (Figure 6A). In contrast, the number of trips does not exhibit a statistically significant relationship with landings (Figure 6B). As suggested previously, since 2018, both vessel and trip numbers have declined alongside landings, suggesting reduced fishing effort potentially induced by a potential decrease in resource abundance.

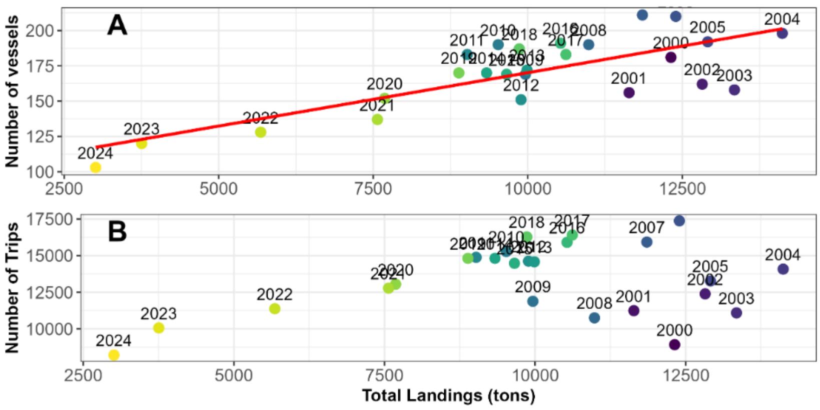

Figure 6. *Relationship of annual number of vessels (A) and trips (B) to annual landings (the line indicates a significant relationship at the conventional threshold of 5%).*

3.2. Proxy of abundance: LPUE

This section presents the temporal evolution of total landings and the fishing effort of the reference fleet over the period 2000-2024, based on SACROIS data and data from the "Calendrier d'activité". The evolution of the number of fishers (Figure 7A) and landings in tonnes (Figure 7B) between 2000 and 2024 shows distinct trends. The number of fishers rose from around 8,000 in 2000 to a first peak of approximately 12,500 in 2004 (increase of 56.3%), before stabilizing at about 10,000 until 2015 (Figure 7A). A second increase occurred between 2016 and 2018, reaching again about 12,500 fishers (increase of 25% compared to 2015), followed by a steady decline to around 9,000 in 2024 (decrease of 28% compared to 2018) (Figure 7A). Landings increased rapidly from 2,500 tonnes in 2000 to a peak of roughly 4,000 tonnes in 2004 (increase of 60%), then remained between 2,500 and 3,000 tonnes until 2015. A recovery is visible between 2016 and 2018 with values close to 3,500 tonnes (increase of 25% compared to 2015), but the trend then sharply reversed, with landings dropping to about 1,500 tonnes in 2024 (decrease of 57% compared to 2018) (Figure 7B). This recent divergence, with a faster drop in landings than in the number of fishers, suggests a decline in the fishery's productivity in recent years.

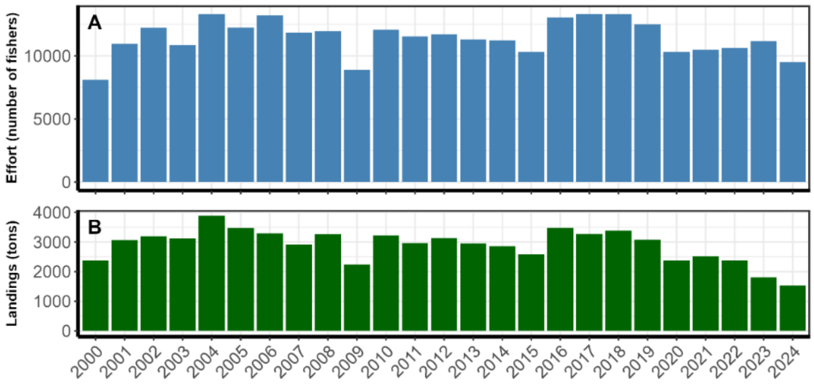

Figure 7. *Annual fishing effort (in number of fishers) (A) and annual landings (in tons) (B) of the reference fleet targeting whelk in the WEC.*

The standardised LPUE, derived from the previously described effort and landings data, shows a gradual decline over the whole period (Figure 8). It falls by more than 40%, from around 264.61 kg/fisher/trip in 2000 to less than 154.8 kg/fishers/trip in 2024 (Figure 8). A notable drop of 26.8% is observed between 2022 and 2023. The raw LPUE, which does not take structural effects into account, follows a similar trajectory but remains consistently higher, highlighting potential biases related to random effects linked to the month and the vessel (Figure 8).

An initial period of decline is observed between 2000 and 2006, followed by a period of relative stability between 2007 and 2019, characterised by moderate inter-annual variations (Figure 8). From 2020 onwards, both indicators decrease sharply, reaching their lowest level in 2024 (around 154 kg/fisher/trip) (Figure 8). This gradual, sharp deterioration in standardised LPUE indicates a significant decline in the abundance of whelks in the WEC, independent of changes in the structure of fishing effort. These results highlight the need to pay particular attention to stock dynamics and status before environmental effects become visible in landings.

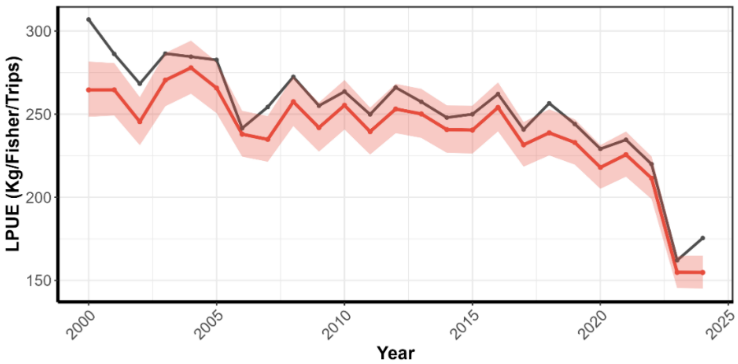

Figure 8. *Annual Landings Per Unit Effort (LPUE) of whelk in WEC (brown = Not standardized; red = standardized; red shaded area = 95% confidence intervals).*

3.3. Sea Surface Temperature and MHWs dynamics in the whelk habitat area

3.3.1. Sea surface Temperature (SST)

The average annual SST in the proxy of the habitat of the whelk in the WEC (ICES rectangles 26E8, 26E7 and 27E8) shows a significant upward trend over the period 1983-2024 (Figure 9A). The linear regression fitted to these data shows a significantly positive slope, estimated at 0.0357 ± 0.0048 °C/year (p-value < 0.001, $R^2 = 0.581$) (Figure 9A). The analysis highlights a gradual increase in temperatures, with a rise of approximately 1.46°C over 41 years (Figure 9A). Monthly temperature trends show great consistency over time: the hottest months (July to September) and the coldest months (February and March) remain the same regardless of the period considered (Figure 9B). During the early period (1983-1988), February and March were characterised by significantly lower temperatures than January, indicating stronger winter cooling in the past.

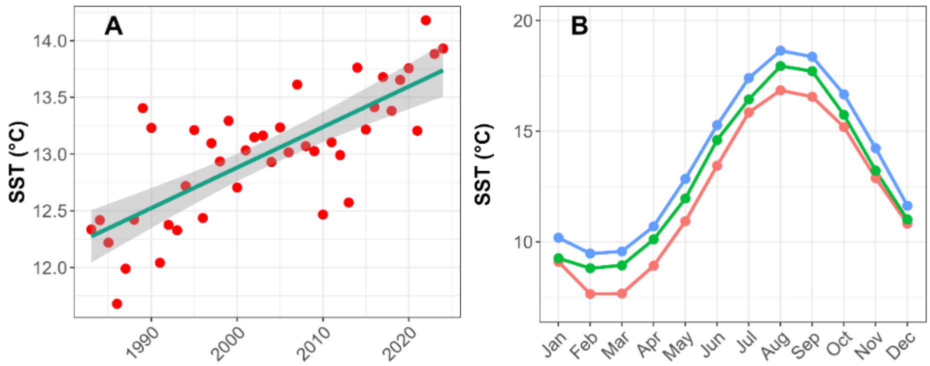

Figure 9. *Annual mean SST (°C) from 1983 to 2024 (A) and monthly SST climatology averaged over three periods (red = 1983 to 1988, green = 2000 to 2004, blue = 2019 to 2024) (B) in the whelk habitat.*

Average SST show a significant upward trend over the period studied (1983-2022) for all seasons (Figure 10). Linear regression analyses show statistically significant seasonal increases in average temperatures (Figure 10). In winter, the mean temperature increased by 0.031°C per year (p-value < 0.001; $R^2 = 0.28$), indicating the lowest seasonal increase in SST, corresponding to an overall warming of +1.25°C since 1983 (Figure 10). In summer, this increase reaches 0.036°C per year (p-value < 0.001; $R^2 = 0.51$), corresponding to a total SST increase of +1.42°C (Figure 10). Spring displays the most pronounced warming trend, with a significant increase of 0.041°C/year (p-value < 0.001; $R^2 = 0.45$), amounting to a total increase of about +1.65°C (Figure 10). Autumn shows a significant increase of 0.035°C/year (p-value < 0.001; $R^2 = 0.48$), corresponding to a total increase of about +1.39°C (Figure 11).

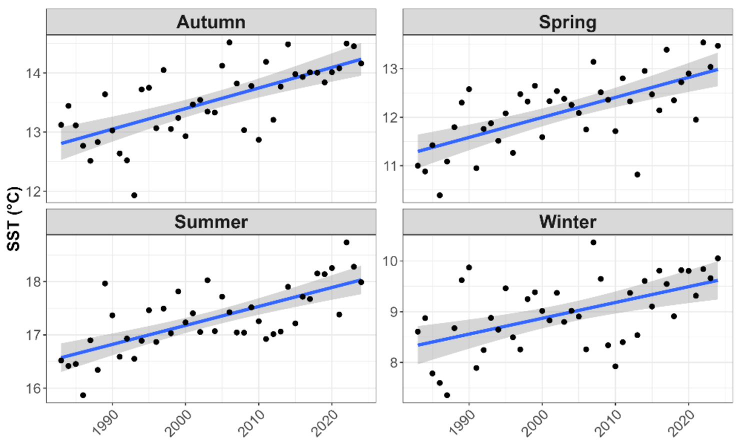

Figure 10. *Seasonal trends in annual average SST from 1983 to 2020 in the whelk habitat of the WEC (blue line = linear trend; grey band = 95% confidence interval).*

3.3.2. Summer MHWs (MHWs)

An analysis of summer MHWs, adjusted for the long-term trend, shows a major change since 2014, with events becoming increasingly frequent and prolonged, 8 years with at least one MHW have been recorded over the past 11 years. This reflects an increased recurrence of warm anomalies even in the absence of average warming (Figure 11). The three characteristics (duration, average intensity and maximum intensity) defining summer MHWs do not show a clear interannual trend.

The year 2003 stands out as an exceptional summer MHW, with a cumulative annual duration of more than 60 days (Figure 11A), an average intensity of more than 1.1°C above the climatological threshold (90^{th} percentile) (Figure 11B), and an average annual maximum intensity of around 1.5°C (Figure 11C). This event far exceeds the other years in the dataset. Outside 2003 (and 2017, which was intense but short-lived), events typically last between 5 and 20 days and show temperature anomalies averaging around 0.9-1.0°C, with maximum intensities between 1.1°C and 1.3°C (Figure 11C).

It should be noted that the effects of MHWs occur in addition to long-term warming. For instance, the average summer temperature in 2017 was around 17.5°C (Figure 11). This was exacerbated by a marine heatwave that summer, with an average intensity of 1.2°C (Figure 11B) and peaking at almost 1.7°C (Figure 11C). Consequently, marine organisms, including whelks, were exposed to temperatures of around 18.7°C for nearly 10 days.

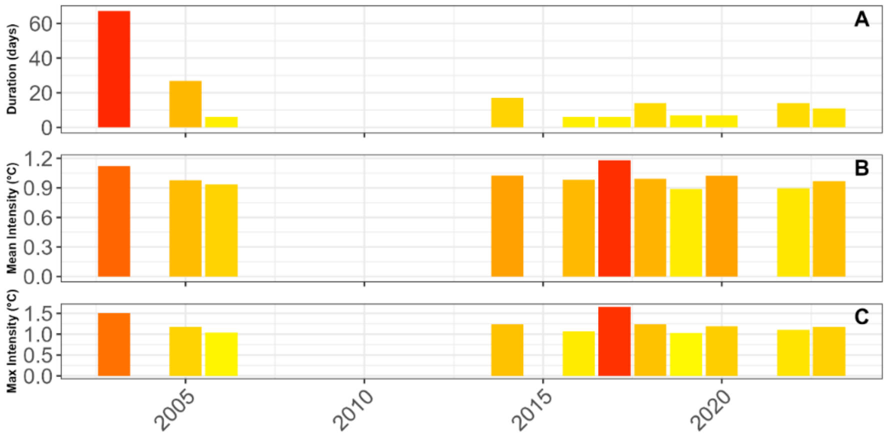

Figure 11. *Annual duration (days) (A), average intensity (°C) (B), and maximum average intensity (°C) (C) of MHWs identified in the WEC whelk habitat (Color intensity represents the relative strength of heatwaves, with darker shades indicating more sever.*

3.3.3. Daily SST and Biological threshold

This exploratory and qualitative approach relies on the literature to identify biologically relevant thermal thresholds for whelks, distinguishing between winter and summer conditions, with the aim of linking temperature variability to stock abundance. The proportion of days below 9.5°C, the threshold identified as triggering whelk spawning, has fallen sharply, from over 40% in the 1980s to 2011 (with occasional lower years such as 1990 and 2007), to a systematic downward trend after 2011, reaching less than 10% in 2022 and 2024 (Figure 12). This contraction of the cold period suggests a significant reduction in the potential breeding window[2].

[2] Reminder: whelks spawn between 9 and 10 °C.

At the same time, the frequency of days above the 18°C threshold, beyond which whelks enter physiological inactivity, has increased sharply (Figure 12). Whereas this threshold was sometimes never reached before 2000, it now systematically affects up to more than 50% of annual days in years after 2018 (except for 2021, when it is less than 25%) (Figure 12).

Figure 12. *Percentage of days of the year above the threshold of 18°C and 9.5°C in the whelk habitat zone (red = above threshold; blue = below threshold).*

<u>3.3.4. Statistical approach focuses on summer conditions</u>

This approach is based on a statistical analysis of summer conditions, aiming to quantify the potential effect of mean summer temperature and/or summer MHWs on the WEC whelk stock, by testing different types of GAMs.The analysis revealed a threshold relationship between summer thermal conditions in year t-1 and the abundance of the WEC whelk stock in year t.

3.3.4.1 Screening nonlinearities

The GAMs models tested, including mean summer temperature (year t−1), the presence of summer MHWs (year t-1), and their interaction, showed that only mean summer temperature (t-1) had a significant relationship with stock abundance in the following year (p-value < 0.05). This result was consistent regardless of the probability distribution used, with the significant effect always being nonlinear. Among the models tested, the one assuming a log-Gaussian distribution provided the best fit to the data (Appendix. 14). This model explains 62.3% of the deviance and has an adjusted R^2 of 0.565. The response curve of the GAM model indicates a decrease in the standardised abundance of whelks with increasing summer temperature (in year t-1) (Figure 13). The binary variable describing the presence of MHWs in year n−1 does not significantly explain the interannual variation in abundance. Neither alone nor in interaction with temperature does it improve the model fit.

3.3.4.2. Identification of summer threshold

A specific threshold was identified at 18.02 °C based on the second derivative analysis of the response curve derived from 200 predicted data points) (Figure 13). This threshold indicates a turning point where the relationship between summer temperature and stock abundance decreased markedly, suggesting an intensified biological response beyond this value.

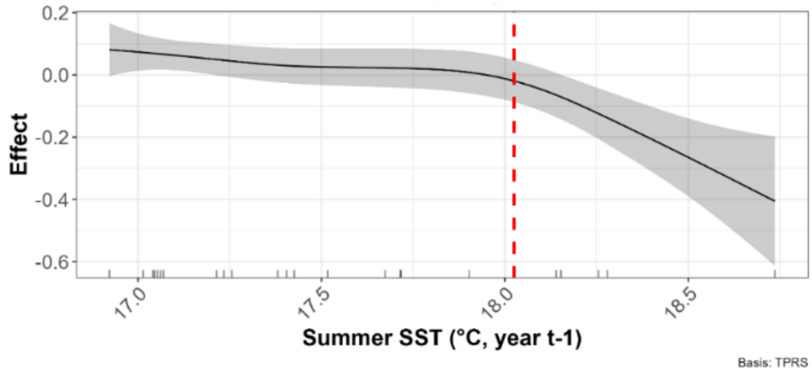

Figure 13. *Effect of the annual mean summer temperature of year n-1 on the LPUE (threshold identified = dotted lines).*

3.5. Stock assessment

3.5.1. Length-Based Indicators

To assess the exploitation status and sustainability of the whelk stock in the Western English Channel, four categories of length-based indicators (LBIs) were examined: conservation of large individuals (Pmega and Lmax5%/Linf), conservation of juveniles (L25/Lmat), optimal yield (Lmean/Lopt), and sustainability in relation to fishing mortality (Lmean/LF=M). The analysis is based on individual length data collected between 2009 and 2025 in the Western English Channel. Retention probabilities derived from the selectivity of the sorting grid were applied in order to isolate the commercial fraction of the landings. Details on the estimation of selectivity parameters (SL_{50}, SL_{95}, Lc) and the fitting procedure are provided in (see section 2.8.2; Appendix 17,18, 19 and 20).

3.5.1.1. Stock Status in 2025

Table 2. *Summary table of LBIs for 2025 with indications of status compared to reference points for ICES length-based method. The colour red indicates that the condition is below the expected value, orange indicates an uncertain condition, and green indicates that the conditions are met.*

Indicator	Conservation (large)	Conservation (large)	Conservation (immatures)	Optimal yield	MSY
	Pmega (%)	Lmax5%/Linf	L25/Lmat	Lmean/Lopt	Lmean/LF=M
Expected value	>0.3	>0.8	>1	aprrox. 1	>1
2025 (mean value)	0 .16	0.83	0.95	0.98	0.96
[low-upp]	[0.04-0.38]	[0.77-0.91]	[0.92-0 .98]	[0.9-1.07]	[0.93-0.99]

Among the conservation indicators in 2025, the L25/Lmat ratio is relatively high (0.95), but still slightly below the threshold of 1, suggesting that a non-negligible proportion of the catch consists of immature individuals (Table 3). The narrow confidence interval [0.92-0.98][3] supports the reliability of this estimate (Table 3).

[3] The confidence interval presented in Section 3.5.1 reflects the uncertainty surrounding of the parameter Linf,.

When it comes to large individuals, the results are more contrasted. The Lmax5%/Linf ratio, which reflects the presence of the largest individuals in the stock, reaches 0.83, above the 0.8 threshold, suggesting some degree of preservation of large individuals (Table 3). In contrast, the proportion of very large individuals (Pmega) is particularly low (0.16), well below the recommended threshold of 0.3, with a confidence interval [0.04-0.38] indicating high variability but an overall unfavourable status (Table 2).

This divergence between the two indicators related to large individuals prevents a clear conclusion about the status of the largest fraction of the stock, highlighting the need to interpret these indicators jointly and with caution. Finally, the exploitation-related ratios Lmean/Lopt (0.98) and Lmean/LF=M (0.96) are close to the sustainability thresholds (~1), suggesting that the stock is currently being exploited at levels approaching, but not fully reaching, optimal and sustainable yield.

3.5.1.2. Conservation (large individuals)

The proportion of mega-spawners (Pmega) consistently remained below the 30% threshold recommended to ensure stock resilience, with maxima < 20% and minima < 10% in 2013 and 2023 (Figure 14A). After a progressive increase between 2013 and 2019, Pmega declined again from 2020 onwards, reaching a second minimum in 2023. The wide confidence intervals reflect strong interannual uncertainty. These low values suggest an alteration of the demographic structure, likely reducing the reproductive potential of the stock. The ratio between the mean length of the 5% largest individuals and L∞ ranged between 0.79 and 0.85 (Figure 14B). With the exception of 2023 (0.79), all years reached or exceeded the 0.8 threshold recommended by ICES, indicating an overall conservation status broadly consistent with sustainable exploitation.

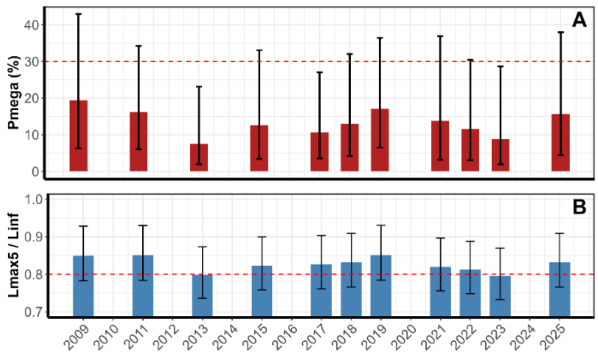

Figure 14. *Annual proportion of megaspawners (A) and Lmax5/Linf (B) over the time series (2009 to 2025) with the threshold recommended by ICES (dotted lines) and confidence intervals (error bars)*

Overall, the two indicators showed similar dynamics: marked minima in 2013 and 2023, and an increase between 2014 and 2019. Pmega appears to be the most conservative indicator, consistently below the threshold, while the ratio of the 5% largest individuals is the most permissive, generally above 0.8. However, the variability of the confidence intervals highlights the importance of integrating uncertainty into the assessment of large size classes.

3.5.1.3. Conservation (immatures)

Between 2009 and 2025, L25/Lmat ratios consistently remained below the sustainability threshold of 1, regardless of whether Lmat was set at 50 mm (0.96-0.99) or 53 mm (0.90-0.93) (Figure 15). This indicates that part of the catch consists of immature individuals. Interannual variability was low, with a decline from 2009 to 2013, stabilization and slight increase until 2021, followed by a drop in 2022 and a rebound in 2023. The temporal pattern mirrors that of large-individual indicators, with aligned minima in 2013 and higher values in 2019-2021, but with a narrower range of variation (Figure 15).

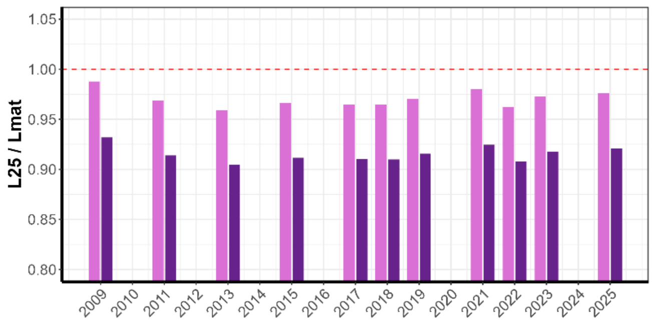

Figure 15. *Annual L25/Lmat ratios over the time series (2009–2025), with ICES recommended threshold values indicated by dotted lines. (Light purple = Lmat set at 50 mm and dark purple = Lmat set at 53 mm).*

3.5.1.4. Optimal yield and MSY

The Lmean/Lopt ratio shows some variability between 2009 and 2025, with values ranging from 0.93 to 0.99 (Figure 16A). All annual mean estimates remain below the threshold value of 1 recommended by ICES (2018). Most values are close or very close to 1, suggesting that the average size of individuals in the catch is near the theoretical optimum that maximizes yield per recruit (Figure 16A). The confidence intervals reflect notable interannual uncertainty, and for all years, there is a possibility that the true ratio may exceed the threshold of 1 (Figure 16A).

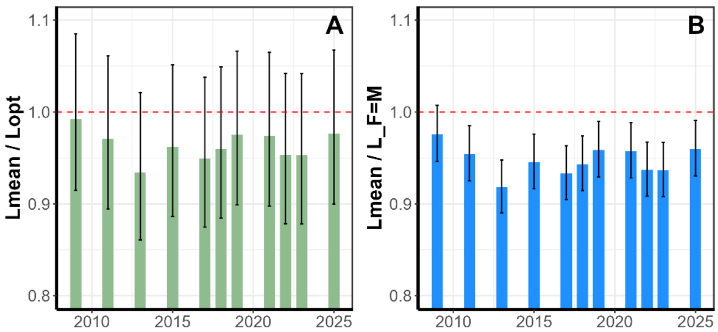

Figure 16. *Annual ratios of Lmean/Lopt (A) and Lmean/LF=M (B) over the full time series (2009–2025), with ICES recommended threshold values indicated by dotted lines and confidence intervals shown as error bars.*

Similarly, the annual Lmean/LF=M ratios are consistently below the reference value of 1, except in 2009 when the upper bound of the confidence interval slightly exceeds this threshold (Figure 16B). These results suggest that the stock has been exploited at levels below those compatible with sustainable fishing during the study period. The confidence intervals for this indicator reflect less variability around the mean for Lmean/Lopt, suggesting that the value of Linf has a greater influence on this ratio. The temporal dynamics of both ratios (Lmean/Lopt and Lmean/LF=M) from 2009 to 2025 resemble those observed for indicators of large-size class conservation (Pmega and Lmean5%/L∞) and for small-size classes (L25/Lmat). All indicators show a similar trend: an initial decline between 2009 and 2013, a gradual increase until 2021, followed by another decline reaching a second minimum in 2023, and a recovery in 2025.

3.5.2. Surplus Production in Continuous Time (SPiCT)

The SACROIS database and standardized abundance index (LPUE) were used. For the catch-based model, residuals show significant autocorrelation ($p = 0.0116$; Appendix. 21), but no bias ($p = 0.2065$; Appendix. 21), and follow an approximately normal distribution ($p = 0.0599$; Appendix. 21). The autocorrelation indicates that the residuals are not independent, reflecting a temporal structure not explained by the model, likely originating from recent years. The model based on the abundance index yields better results: no autocorrelation ($p = 0.9549$; Appendix. 21), no bias ($p = 0.5923$; Appendix. 21), a distribution close to normal ($p = 0.2233$), and no retrospective pattern detected (Mohn's rho < 0.2; Appendix. 22). Sensitivity tests also confirm the robustness of the model: all 10 runs converged with stable estimates (Appendix. 23). Uncertainty remains moderate: B/BMSY = 0.66 [0.33-1.30] and F/FMSY = 0.54 [0.28-1.04]. In 2025, biomass is therefore on average 34% below BMSY, while fishing mortality remains 46% below FMSY (Appendix. 24). This indicates that, although the stock is currently below the biomass level corresponding to maximum sustainable yield, it is not subject to excessive fishing pressure.

Catches have declined since the mid-2000s (Figure 17A). The SPiCT model estimates an average MSY of 8,350 tons (95% CI: 6,370-10,950). From 2000-2019, catches were mostly above this level, indicating overexploitation. Since 2020, they have fallen below MSY, suggesting potentially sustainable levels. Between 2008-2021, catches lie within the MSY uncertainty range, making exploitation status unclear. Before 2008, caches exceeded MSY; after 2021, they are clearly below it (Figure 17A). The evolution of the F/FMSY ratio refines the interpretation of exploitation trends (Figure 17B). From 2000 to 2019, this ratio remained mostly above 1, reflecting fishing mortality exceeding the sustainability level, consistent with catches above MSY (Figure 18B). In 2005, the ratio peaked at around 1.5, indicating particularly high fishing pressure that year (Figure 17B). From 2018 onwards, a gradual decline in the ratio was observed. In 2024, it is estimated at 0.54 [0.28-1.04], suggesting that fishing pressure is likely to be below the sustainability threshold, although the credibility interval does not rule out the possibility of it being exceeded (Figure 17B).

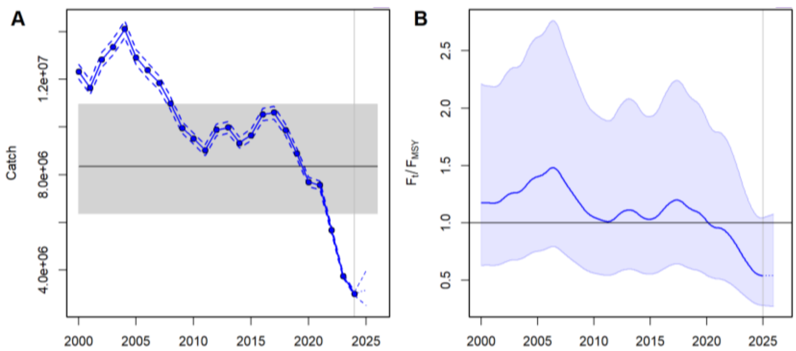

Figure 17. *Evolution of catches (B) and F/FMSY (B) over the 2000 to 2024 time series with the average value of MSY (solid line) and 95% CIs (grey band)*

Between 2000 and 2005, the B/BMSY ratio ranged between 1.3 and 1.4, clearly above the sustainability threshold, indicating that biomass was well above the level required to achieve maximum sustainable yield (Figure 18A). From 2006 to 2020, the ratio remained slightly above 1, suggesting stocks were maintained just over the BMSY level. From 2018 onwards, a marked decrease is observed, reflecting a

gradual decline in biomass. In 2024, the ratio is estimated at 0.66 [0.33-1.30], indicating that the stock is likely below the level needed to produce the maximum sustainable yield (Figure 18A).
The Kobe plot (Figure 18B) illustrates the joint evolution of fishing mortality (F) and biomass (B) in relation to their respective sustainability levels. The stock is mainly in the upper yellow zone, with biomass close to BMSY but mortality above FMSY (Figure 18B). A gradual decrease in biomass is observed, leading the stock into the red zone at certain times, reflecting a situation of overfishing and depleted biomass (Figure 18B). A reduction in fishing mortality is visible, moving the stock towards the lower yellow zone. At the end of 2024, it is in this zone, indicating mortality below FMSY, but biomass still below BMSY (Figure 18B).

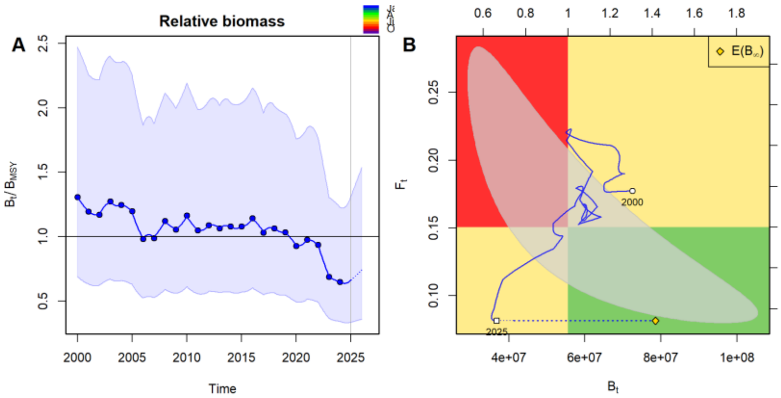

Figure 18. *Trends in B/BMSY (2000-2024, solid line = MSY, blue band = 95% CI) (A) and Kobe plot showing the joint dynamics of F/FMSY and B/BMSY with associated uncertainty (grey envelope) for the WEC whelk stock (B).*

4. Discussion

4.1 Understanding whelk stock decline: the role of fishing and shifting ocean conditions

The results indicate a concerning state of the whelk (*Buccinum undatum*) stock in the WEC. A decline in abundance of around 41% has been observed since 2000, including a 27% drop between 2022 and 2023. The reduction in catches, estimated at around 70% over the past six years, likely linked to the decline in abundance, has led to a decrease in fishing effort. This dynamic suggests at least a twofold reduction in fishing mortality, consistent with SPiCT model estimates via the F/FMSY ratio.

Over the past six years, fishing mortality has declined, yet whelk stock abundance continues to decrease suggesting a possible delayed effect from historically intense exploitation in addition to a very likely warming effect (discussed hereafter). This ongoing decline may be, in part, due to the sensitivity of whelk to overfishing. Whelk exhibits biological traits that heighten its vulnerability: low fecundity, late maturation, limited interpopulation migration, and strong spatial variability in life-history parameters (Shelmerdine *et al.*, 2007; Ashfaq *et al.*, 2019). Between 1993 and 2018, landing exceeded the average CMSY estimated by the SPiCT model (8,350 tonnes), peaking at nearly 15,000 tonnes in 2004. However, data for the 1984-2000 only includes landings from Normand fishers (with the addition of Jersey landings from 1996 to 2000). Since Breton fishers also operate in this area, it is highly likely that landings during this period are underestimated, suggesting that the CMSY threshold was exceeded well before 1993. This surge in exploitation is linked to the growth of the Asian market in the 1990s, which

drove high demand for whelks (Fahy *et al.*, 2000). A decline in landings and fishing mortality was recorded after 2004, possibly in response to management measures implemented to limit fishing effort (Appendix. 3). Between 2005 and 2018, estimates from the SPiCT model suggest that landings, biomass, and fishing mortality were close to the maximum sustainable yield (MSY). Over the 2009-2025 period, LBI indicators reveal an alarming conservation status for large individuals, despite substantial uncertainty (discussed later). These individuals play a key role in stock renewal, as their size is positively correlated with their spawning capacity (Valentinsson, 2002). The status of immature individuals is also degraded, regardless of uncertainty over the size at maturity. The proportion of immatures landed remains high. Landing individuals before their first reproduction undermines the species' reproductive potential.
Concurrently, a gradual increase of approximately 1.5 °C in sea surface temperature has been observed since 1983 in the whelk's habitat in the WEC. This warming may extend inactivity period and shorten spawning windows, directly impacting recruitment (Figure 13). In some whelk populations, rising temperatures correlates with reduced egg production per spawn (Hegron-mace *et al.*, 2017), lower hatching success, and accelerated intracapsular larval development (Smith *et al.*, 2013)

However, the transferability of these thermal thresholds to the WEC stock remains uncertain, as this population may have developed adaptations to the higher thermal conditions of this region. Nonetheless results show that the average summer temperature of the previous year may play a significant role in shaping whelk abundance, particularly under the emerging thermal regime now characterizing the area. The analysis reveals that higher summer temperatures are associated with a marked decrease in abundance, particularly beyond the critical threshold of 18.02 °C, highlighting the importance of integrating delayed effects of environmental conditions into stock assessments. This finding corroborates the previously identified threshold for the Danish stock (Nielsen, 1974). The lengthening of the inactivity period could indicate prolonged thermal stress. Under such conditions, it is well established that the species allocates an increasing share of its energy to physiological maintenance (Alfonso *et al.*, 2021), at the expense of movement and feeding (Brett, 1956).

The seasonality of whelk landings suggests a reduction in feeding activity, with individuals being less frequently caught in pots during the summer. According to fishers, this lower catchability is due to whelks burrowing to seek a thermal refuge, a behaviour already observed in other molluscs (Block *et al.*, 2013). Moreover, the monthly distribution of landings has shifted between 2000-2006 and 2018-2024, with summer months now representing a smaller proportion of total landings. Fishers report catching far fewer whelks in summer than in the past, leading them to adjust their fishing strategies in response to a less available and physiologically constrained resource. Similar thermal effects on feeding and activity have been observed in other species, such as sockeye salmon (*Oncorhynchus nerka*) above 21.1 °C (Donaldson and Foster, 1941), Atlantic cod (*Gadus morhua*) (Castonguay and Cyr, 1998), and European seabass (*Dicentrarchus labrax*) (Koumoundouros *et al.*, 2002), where high temperatures reduce locomotor activity, increase stress, and limit homeostatic capacities, potentially increasing mortality (Kroeker *et al.*, 2014; Genin *et al.*, 2020). Comparable effects have been reported in gilthead seabream (*Sparus aurata*) exposed to high temperatures: pronounced oxidative stress affects vital organs such as the liver and muscles through increased antioxidant enzyme activity, impairing survival, growth, and the ability to move in search of food (Madeira *et al.*, 2016).

The whelk, a boreal ectothermic species located at the southern edge of its distribution range, is exposed to extreme thermal conditions. Under the emerging thermal conditions, these factors can alter its metabolism and, particularly in recent years, contribute to reduced productivity. Studies on American and Irish Sea populations have shown that increasing temperatures influence growth: it tends to be stimulated in early life stages but becomes detrimental in older individuals (Emmerson *et al.*, 2020; Borsetti *et al.*, 2021).
However, the seasonality observed in whelk landings may not be explained solely by a reduction in locomotor activity linked to temperature, but also by more subtle effects on feeding behaviour. By analogy with other species, temperature can influence gustatory receptivity, as in the grass carp (*Ctenopharyngodon idella*) and the stellate sturgeon (*Acipenser stellatus*), where the sensitivity of taste receptors to various amino acids varies with temperature, contributing to seasonal changes in diet (Kasumyan and Døving, 2003). It can also alter feeding frequency and rhythm, as observed in Atlantic salmon (*Salmo salar*), which feeds mainly during the day at temperatures above 6 °C but switches to predominantly nocturnal feeding below this threshold (Fraser *et al.*, 1995), or even influence the circadian rhythm of locomotion, as in zebrafish (*Danio rerio*) (Hurd *et al.*, 1998). If such mechanisms occur in whelks, they could affect the efficiency of daytime pot fisheries using bait during the summer period, thereby contributing to seasonal variations in catches.

In the statistical framework developed in this study, no effect of summer MHWs, as defined in this study (initially defined in Hobday *et al.* (2016)), was detected on the proxy of the stock abundance. These events, recurrent since 2014, occur abruptly and may elude the sensitivity of the statistical methods used in this study. It is also possible that the long-term summer trend has already exceeded the species' tolerance thresholds, making any additional effect from such extremes marginal. In contrast, a long winter marine heatwave could reduce the reproductive window, thereby affecting reproductive potential. A similar spring event could accelerate larval development or enhance predator activity, potentially impacting recruitment success (Smith *et al.*, 2013).
Other environmental and biological factors may also contribute to the decline in productivity of the WEC whelk. While temperature increase is recognized as a major driver, global change also leads to ocean acidification. This acidification reduces the availability of calcium carbonate, making it more difficult for calcareous-shelled species to form solid structures, thereby increasing their vulnerability (Kroeker *et al.*, 2014).

The WEC whelk stock is showing signs of concerning decline, likely resulting from the combined effects of fishing pressure and climate change, whose relative influence varies over time. This dual pressure is particularly worrisome because fishing and climate change interact in shaping fishery productivity: overexploitation reduces biodiversity and alters the demographic and spatial structure of populations, thereby increasing their sensitivity to climate change (Brander, 2007). Climate change can affect stock productivity through both direct and indirect mechanisms. Direct effects include impacts on reproduction, growth, and survival (Smith *et al.*, 2013; Hegron-mace *et al.*, 2017; Borsetti *et al.*, 2021), while indirect effects operate via changes in net primary production or predation pressure (Brander, 2007).
In this context, reducing fishing mortality remains an important management lever, even if the species is no longer considered overexploited according to the MSY estimated by SPiCT. However, given po-

tential changes in productivity under current environmental conditions, the reference points themselves, including MSY, may need to be re-evaluated. This would allow management to account for observed changes in stock productivity, interannual variability, and extreme climate events (Brander, 2007; Serpetti *et al.*, 2017).

4.2 Limits and Ways Forward

Some limitations apply to this study, notably concerning the estimation of the biological parameters that are critical for reducing uncertainties in the in the stock assessment approaches developed herein, and for advancing the development of additional assessment models in the future.

The size at maturity (Lmat) of the WEC whelk remains uncertain. The BestClim project estimated it at 50 mm (Hegron-mace *et al.*, 2017), while C. Heude-Bertelin (2011) reported a higher value of 53 mm. This uncertainty is compounded by the fact that most individuals are sampled in April-May, when females have just spawned. It is then difficult to distinguish individuals in sexual rest characterized by regressed reproductive organs following spawning, from those that are not yet reached sexual maturity. New estimates of size at maturity, produced within the framework of the CCLIMBUP project, by targeting the end of gametogenesis in autumn and supported by both qualitative and quantitative histological analyses of reproductive effort, are expected to significantly reduce current uncertainty. Growth dynamics and associated biological parameters remain also a major source of uncertainty in the assessment of the WEC whelk stock. Existing estimates of the length-age relationship, such as those derived from the BestClim project (Hegron-mace *et al.*, 2017), are based on a limited sample size (n = 39), making key parameters like Linf particularly uncertain. This limitation hampers the development of robust stock assessment models, especially those requiring growth parameters or age structured approaches. To address this gap, the CCLIMBUP project is undertaking a more comprehensive analysis based on statolith readings (calcified structures used to age whelks; Hollyman, 2017) from 140 females and 140 males. This approach will enable the construction of a more precise and reliable length-age relationship, while also investigating the influence of environmental conditions on growth through fine-scale analysis of annual increments (Borsetti *et al.*, 2021).

In addition, the LPUE should be interpreted with caution due to inherent uncertainties associated with the fishing effort. Using the number of fishers onboard as a proxy for fishing effort rather than the number of pots deployed - unavailable in our database - introduces potential bias. Although regulations stipulate that the maximum number of pots permitted onboard is proportional to crew size, it cannot be assumed that all whelk vessels consistently utilize the full quota of pots allowed. This variability introduces potential bias in estimating actual fishing effort and, consequently, in the LPUE. In this study, efforts were made to control catchability, however variation in catchability is another source of uncertainty. Despite the application of several filtering steps aimed at accounting for known sources of variation (Appendix. 7), catchability remains influenced by factors such as environmental conditions, gear efficiency, and fisher behaviour. These uncontrolled elements introduce residual variability.

In the WEC, whelk habitat is approximated using the fishing grounds identified from georeferenced data of commercial fishing vessels. These data suggest areas of higher whelk density, but they are influenced by fishing strategies (Dowling *et al.*, 2015), by constraints related to cohabitation with other fleets such as the scallop fleet, since fishers avoid setting strings in areas where dredges operate to prevent gear damage, and by logistical limitations, as most vessels are under 12 m in length. Furthermore, a significant proportion of the fleet lacks VMS or AIS coverage, as legislation does not require it (Shelmerdine, 2015). As a result, this study provides only a partial picture of the activities of the whelk fleet, a common challenge in such studies (Shepperson *et al.*, 2018). Moreover, these smaller vessels cannot venture far offshore as they lack the fuel capacity for trips exceeding one day while remaining economically viable. Thus, even though the species is coastal, there may be individuals further offshore, as a new offshore whelk license has recently been introduced to compensate for declining landings (CRPMEM, 2024). Future work should integrate these georeferenced data with scientific surveys from minimally exploited zones to refine habitat estimates.

Since this is a coastal species, the use of a satellite product with a resolution of around 25 km, such as OISST, introduces uncertainty in local temperature estimates, which may limit the description of fine-scale thermal dynamics. A limitation of this study is that the dynamics may not be fully captured with the datasets currently used. The resolution of commonly used products such as OISST may smooth the intensity and location of coastal thermal fronts. Higher-resolution satellite datasets such as MUR (~1 km global daily SST) can better represent these features. For instance, off Pisco (Peru), the seasonal SST cycle measured with MUR shows a greater amplitude than in lower-resolution datasets, highlighting the added value of high-resolution products (Vazquez-Cuervo *et al.*, 2013).

An important limitation of this study lies in the very definition of a marine heatwave, which currently relies solely on a scientific consensus. When considering the impact on a species' biology, it becomes necessary to rethink this definition, as it is presently based on exceeding the 90th percentile temperature for at least five consecutive days (Hobday *et al.*, 2016). However, nothing prevents us from thinking that the impact on an ectothermic species might only be felt after ten days, or when the mean exceeds the 95th percentile. It is certain that the species has its own "definition" of a heatwave, which is not necessarily the one set out in the literature (Hobday *et al.*, 2016). Other fundamental questions such as the ideal period over which to calculate the climatological mean, or whether to remove the trend and how to do so, are subject to ongoing debate in the literature (Farchadi *et al.*, 2025). All of this may also explain why no signal was retained for the abundance of the WEC whelk stock, as AIC did not support the inclusion of summer MHWs presence.

4.3 Perspectives

A first line of research will aim to improve the understanding of stock abundance dynamics. The ongoing standardisation of CPUE data collected by SMEL will provide a key tool to refine the temporal monitoring of the resource. These data, gathered between 2009 and 2025 within the framework of several projects (Gestion durable des pêcheries, BULOCLIM, BESTCLIM, ESHANO, MECANOR, COGECO and CCLIMB UP) and by different stakeholders (SMEL, CRPMEM, IFREMER), constitute a solid but still incomplete basis to characterise stock dynamics. In addition, the integration of data from Jersey would provide an opportunity to expand the spatial scale of the analysis and to strengthen the robustness of the identified trends.

A second line of research will focus on improving knowledge of the link between seawater temperature and the species' biology. Controlled-environment experiments will expose different size classes to

thermal gradients, with and without marine heatwaves (MHWs), in order to assess the effects of temperature on key processes such as maturity, behaviour (burrowing, inactivity), spawning, and mortality. These simulations will provide critical insights into the potential impacts of long-term warming and MHWs on English Channel whelk populations.
In parallel, growth will be investigated through statolith analysis. Examining a balanced sample of females and males will allow the establishment of a robust length-age relationship, while also assessing the influence of environmental conditions on growth via the fine-scale study of annual increments. This approach will help clarify the variability of growth trajectories and their ecological drivers.
Moreover, an integrative perspective on the species' physiology will be developed. A de novo transcriptomic approach, made necessary by the absence of a reference genome, will allow the identification of metabolic pathways and physiological functions affected by thermal stress. This will provide a comprehensive view of the underlying biological mechanisms, bridging individual and population level responses and contributing to a better understanding of the consequences of climate change on whelk stocks.

Controlled experiments conducted within the CCLIMB UP project will provide essential insights to help define a species-specific concept of marine heatwaves for the whelk in WEC. These experiments will make it possible to test absolute and seasonal thermo-physiological thresholds (around 18 °C in summer, *section 3.3.4.2* ; 9-10°C in winter, Kideys *et al.*, 1993) in relation to different biological phases. They will also help clarify which durations and intensities of exposure are truly relevant (beyond the current scientific consensus on MHW definition) still uncertain but crucial for tailoring this concept to the species' ecology and for better understanding its influence on stock abundance.
Incorporating environmental conditions into the stock assessment of the western English Channel whelk represents a promising avenue in the context of climate change, particularly given the increase in marine heatwaves (MHWs) observed since 2014-2016. Two main approaches can be considered.
A first, more pragmatic and readily applicable option relies on indirect approaches. These consist in estimating productivity and biological reference points as time-varying rather than constant parameters. Following the framework developed for surplus production models such as SPiCT, this can be achieved by introducing temporal dynamics of productivity (r) and carrying capacity (K) (Mildenberger *et al.*, 2025). Applied to whelk, this would allow a comparison of two contrasting periods (2000-2015 vs. 2016-2024), the latter corresponding to a regime shift associated with more frequent MHWs. Such an approach would lead to dynamic reference points (BMSY, FMSY) that are more representative of recent environmental conditions. Complementarily, length-based indicators (LBIs) could be extended to incorporate parameters known to vary with temperature, such as size at maturity and growth.
A second, more ambitious but also more demanding option involves direct approaches. These aim to establish explicit links between environmental variables and key biological processes such as recruitment or natural mortality. In line with previous work demonstrating the influence of the Mid-Atlantic cold pool on yellowtail flounder recruitment (Miller *et al.*, 2016), similar models could be developed for whelk by incorporating co-variates such as SST anomalies or MHW indices into age- or size-structured models. This would make it possible to quantify directly the effect of thermal stress on recruitment success. However, such an approach requires two essential conditions: the development of an age- or size-structured model for whelk, and the establishment of a statistically robust link between environmental variables and biological parameters.

The findings of this study highlight the sensitivity of the whelk to thermal variability and its vulnerability to marine heatwaves, raising important questions for the future management of the fishery under climate change. One first avenue concerns the revision of the minimum landing size (MLS). The threshold currently set by the European Union at 45 mm, unchanged since 1983, appears inconsistent with biological knowledge, as several studies (Heude-Berthelin *et al.*, 2011; Haig *et al.*, 2015; Hegron-mace *et al.*, 2017) indicate that the size at first maturity often exceeds this value. This implies that some individuals are harvested before reproducing at least once. Although undersized whelks are sorted using selective grids and mostly returned to the sea, post-release survival rates remain unknown. If survival is low, this practice could jeopardise recruitment. In this context, an increase in MLS would represent a precautionary approach, but further research on reproductive biology and discard survival is required before such a regulatory change can be implemented.

A second perspective lies in the introduction of catch quotas. The evidence for time-varying productivity of the stock suggests that static management rules may not be sufficient. Quotas defined in relation to biological reference points that account for interannual variability in productivity could provide a more adaptive framework. This would allow harvest levels to be adjusted according to both the state of the stock and the environmental conditions of the previous year, thus aligning management with the principles of adaptive fisheries governance.

From a spatial standpoint, the heterogeneous nature of coastal thermal dynamics in the Western English Channel points to the possibility of localised closures. Some areas may be disproportionately affected by marine heatwaves, and restricting fishing in these zones could help preserve critical habitats. This requires a finer understanding of spatial dynamics, which could be achieved by combining scientific survey data with high-resolution satellite products such as MUR (1 km). Such integration would enable the mapping of realistic habitats suitable for this benthic species and the identification of priority conservation areas.

Temporal closures could also be envisaged, especially during the summer months when marine heatwaves are most frequent and physiological stress for whelks is likely to be greatest. These closures could be permanent for certain months or activated adaptively in years when heatwaves occur. In the longer term, if robust links between temperature and population indicators such as CPUE, recruitment, or growth are established, environmental variables could be incorporated into short-term forecasting models. This would make it possible to set annual quotas based not only on stock dynamics but also on expected environmental conditions, bringing the fishery closer to a truly adaptive management system.

Taken together, these advances, coupled with a better understanding of productivity changes linked to climate change, will pave the way for the implementation of more comprehensive and fuller analytical stock assessment models capable of integrating directly or indirectly environmental effects. These tools will enable the proposal of adaptive, realistic, and effective management plans that reconcile ecological sustainability with the socio-economic viability of the WEC whelk fishery.

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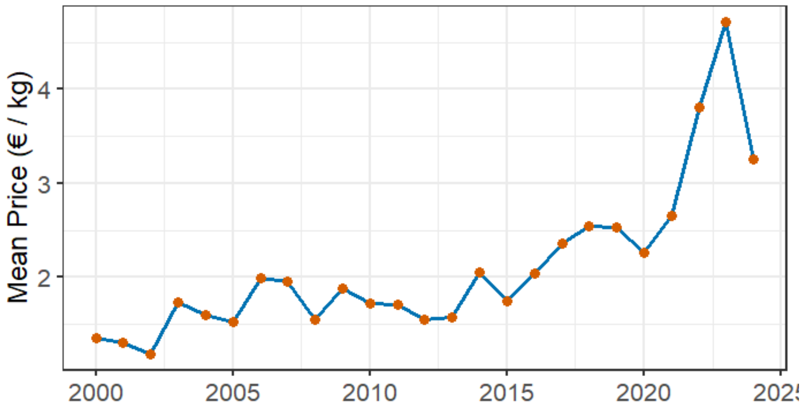
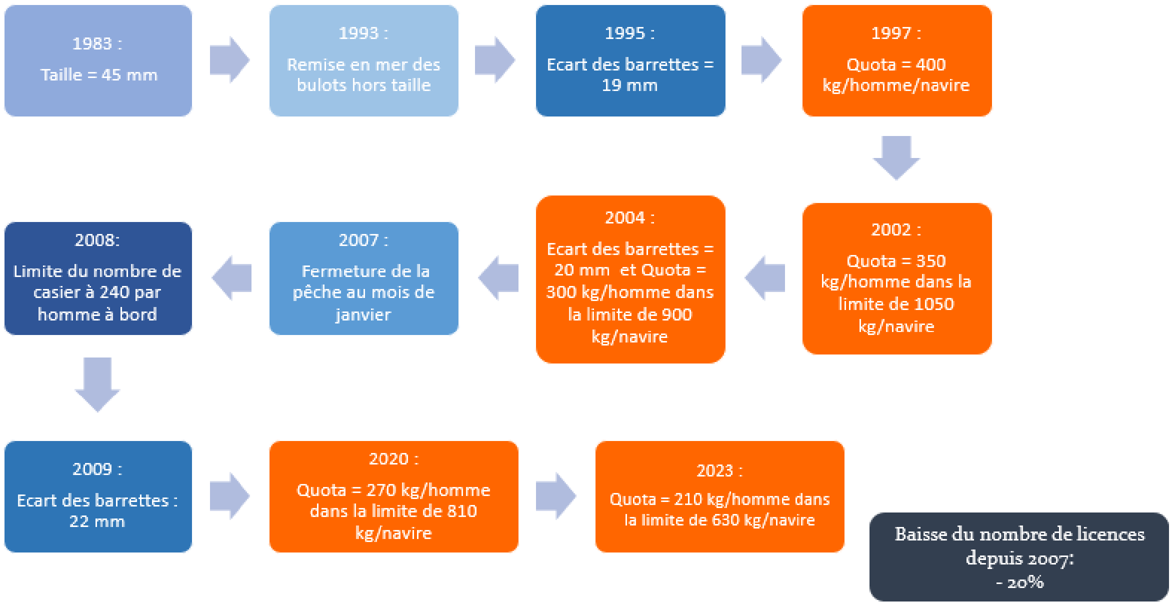
APPENDIX

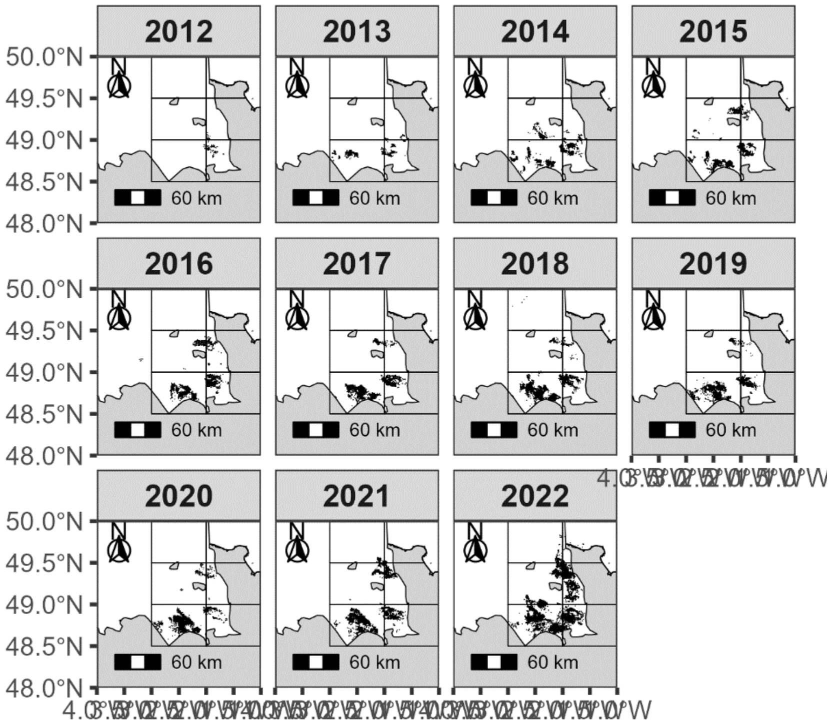
Appendix 1. *Example of a whelk fisher setting up his longline with traps and Whelk pots fixed to a concrete plate used as ballast (Brutel-Philip et al., 2014)*



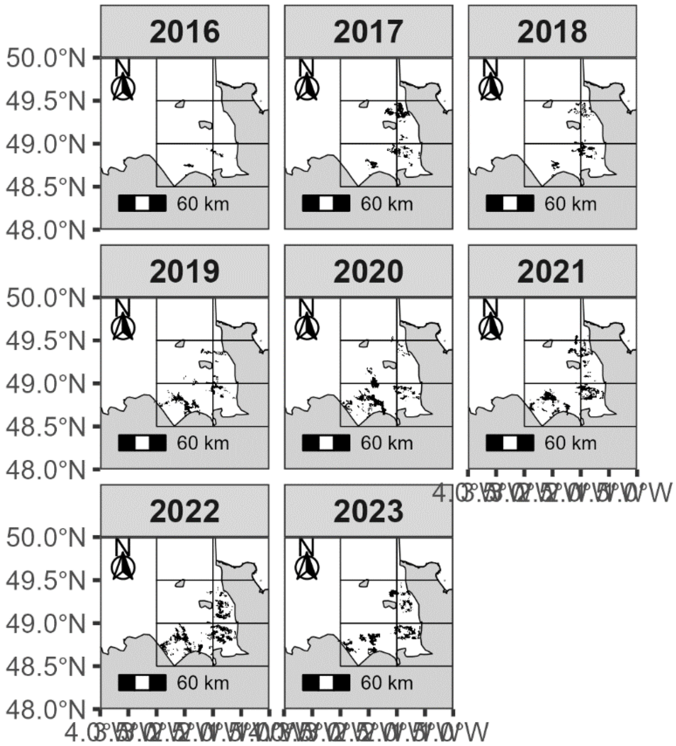
Appendix 2*. Annual mean price (euros/kg) over time series 2000 to 2024 (SACROIS)*



Appendix 3. *History of regulatory management plans concerning the whelk stock in the WEC (CRPMEM).*



Appendix 4. *VMS data of vessels landing whelk in the WEC for each year*



Appendix 5. *AIS data of vessels landing whelk in the WEC for each year*

Appendix 6. *Description, Filtering, and Correction of Whelk Landings Data in the Western English Channel (SA-CROIS, 2000-2024)*

In SACROIS, each line represents a trip/species/place of activity, including the trip identifier, the vessel ID number, the dates of departure and return, the time spent at sea, the type of fishing activity, the gear used, the locations of the ports of departure and return, the ICES statistical area of activity, the volume and price of landings, and the characteristics of the vessel. The data cover the period from 2000 to 2024. A first filtering step was applied to retain only whelk landings in the WEC under French flag, to obtain a first estimate of French landings.

Some errors remain due to the overlap of ICES statistical squares between the WEC and EEC areas, leading to inconsistencies in the recording of landings. For example, whelk caught in WEC have sometimes been attributed to stock EEC and vice versa. In order to correct these errors, ports of departure were used as a criterion, as whelk fishermen operate on a daily basis and do not go round the Cotentin to fish. After correction, 12.72% of the landings originally recorded in the EEC were reallocated to the WEC, while 0.17% of the landings from the WEC were reallocated to the EEC as a proportion of the total gross landings from the WEC.

Preliminary analysis of the landings data indicated that anomalous data were reported in 2011 from a vessel that landed more than 1,200 tonnes of whelk for some fishing trips, which represent highly aberrant values for a 12m whelk vessel. These data were therefore deleted. They represented 1.14% of the total landing in the WEC. These data are therefore considered to be our raw whelk landings data for the WEC.

Appendix 7. *Definition and Filtering of the Reference Fleet for the Whelk Fishery (SACROIS, 2000-2024)*

In this study, LPUE was calculated using catch data extracted from the SACROIS database (see section 2.4). These data are available at the fishing trip level.
In order to obtain the most reliable LPUE proxy, it was necessary to filter the landings data by creating a reference fleet that reflected the real conditions of the fishery:

- Only vessels using fishing pots specifically targeting whelk were selected, representing 99.28% of landings. This choice makes it possible to exclude other trips with different fishing practices and catchability of the resource, thus ensuring the homogeneity of the data and avoiding bias.

- Secondly, only the 3 statistical squares confirmed by AIS and VMS data, and associated with the highest whelk landings, were retained. This approach minimizes area-related bias while ensuring the best possible representation of the fishery. This filtering resulted in the loss of 35.57% of the landings but ensures that the remaining data are consistent and reliable for analysis.

- Only trips conducted between February and June were retained to avoid catchability bias associated with whelk inactivity during warmer months (Hegron-Macé *et al.*, 2017). January was excluded due to a fishery closure in 2007, which could introduce artificial temporal bias. This seasonal filtering resulted in a 46.83% reduction of the remaining dataset, with 34.01% of total landings ultimately retained.

- To improve the reliability of LPUE estimates, only vessel-year combinations with fishing activity in at least four months between February and June were retained. This criterion ensures that selected vessels exhibit consistent effort during the core fishing season, reducing bias from irregular or opportunistic fishing behavior. This step resulted in a 5.47% reduction of the dataset at this stage. In total, 32.15% of the original landings were retained following this filtering step.

- Unrealistic catch values were excluded by removing observations above the 99th annual percentile. This threshold helps eliminate outliers while preserving the core distribution, thus improving the robustness of LPUE estimates. This step resulted in a loss of 7.48% of the data. In total, 29.75% of the initial landings were retained after this filtering.

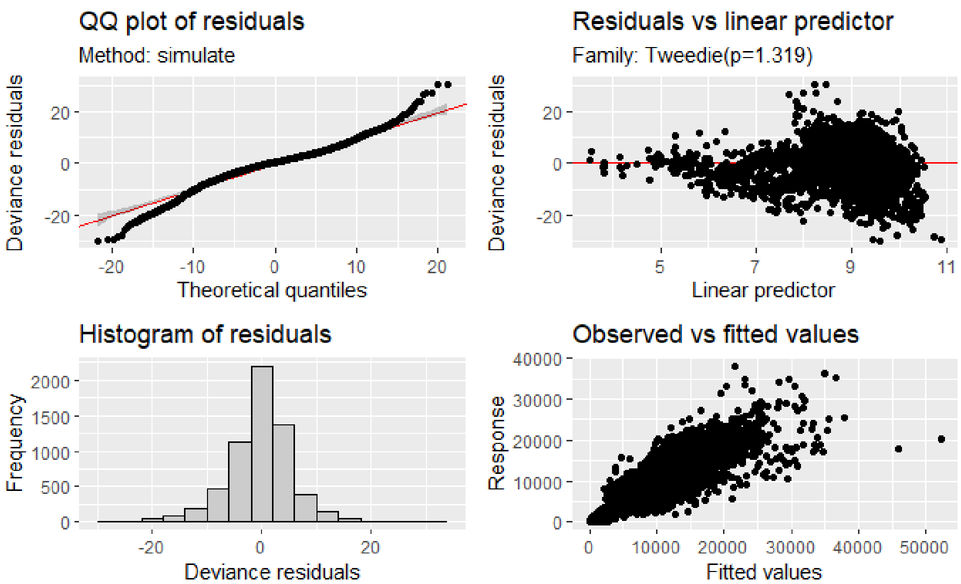
To obtain a consistent measure of fishing effort, absent from SACROIS data for vessels using pots, the vessel activity calendar was used in this study. This calendar, produced annually by the SIH through an exhaustive reconstruction of vessel activity, covers all vessels registered in the national fleet register (FPC). It provides monthly information on whether each vessel was active, the metiers practiced (*i.e.,* gear-species-area combinations), the main home port, the average number of crew members onboard, and the number of sea or fishing days.

Fishing effort was approximated using the crew size, based on the assumption that the maximum number of pots authorized on board is directly linked to the number of crew members. This approach enables a standardized and coherent estimation of fishing effort, especially in cases where trip-level data are unavailable or insufficient for vessels using pots. A filter was applied to exclude trips reporting more than four crew members on board. Such a crew size is considered unrealistic for vessels targeting whelk with pots and likely reflects data entry errors or anomalies. Moreover, beyond four crew members, the number of pots allowed on board is no longer strictly proportional to crew size, thus weakening its use as a proxy for fishing effort. The dataset was therefore restricted to trips with four or fewer crew members, in line with typical vessel configurations in the whelk fishery. This step improves the consistency and reliability of the effort indicator. As a result, 0.43% of landings were lost at this step.

Effort data were merged with the catch data based on id number of vessel and month-year. Some data were lost due to missing effort information for certain trips (2.76% of landings) were lost at this step. At the end, 29.26% of the total initial landings were retained.

Model	AIC
Tweedie	**112 584**
Gamma	**114 781**
Log (gaussian)	**115 723**

Appendix 8. *AIC of GAM models according to the tested probability distributions*



Appendix 9. *Diagnostic plots of the selected Tweedie GAM model used to construct the LPUE.*

$$Y = \exp(y + 0.5*\sigma^2)$$

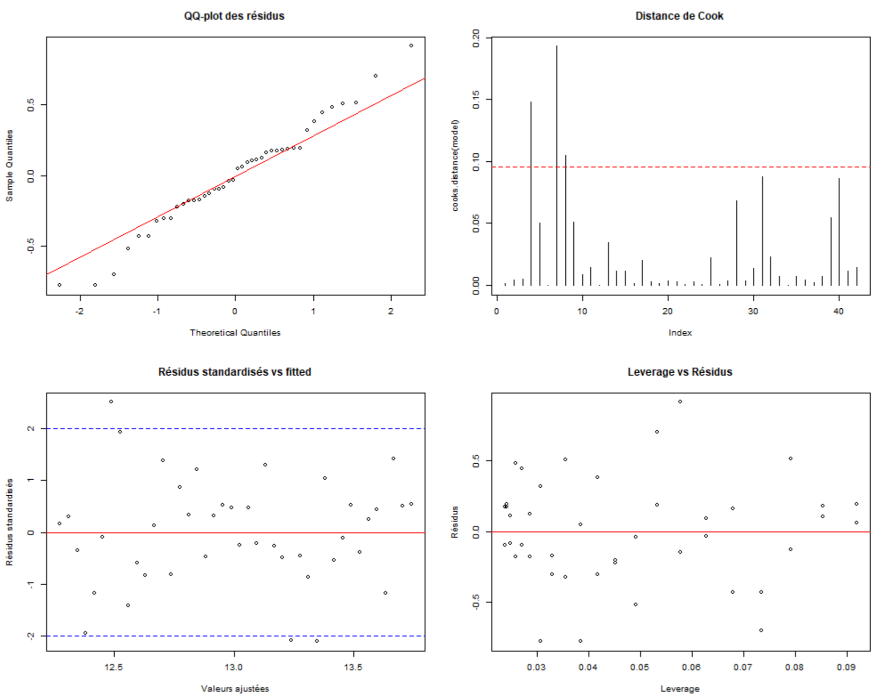
Where :

- Y= estimate of the mean on the response scale,
- y = prediction on the link scale (log),
- σ = standard error of the prediction on the link scale.

Appendix 10. *Laurent's Correction*

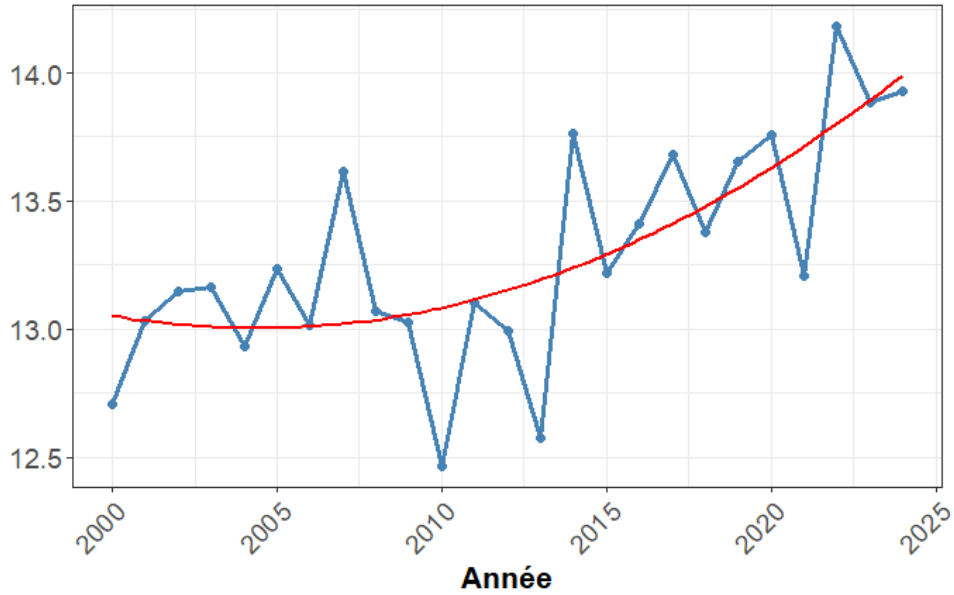
	df	AIC
model_poly2	4	43.06938
model_lm	3	41.09521

Appendix 11. *AIC of the linear model and the second-degree polynomial model for mean_temp ~ year.*



Appendix 12. *Diagnostic plots of the linear model for mean_temp ~ year.*

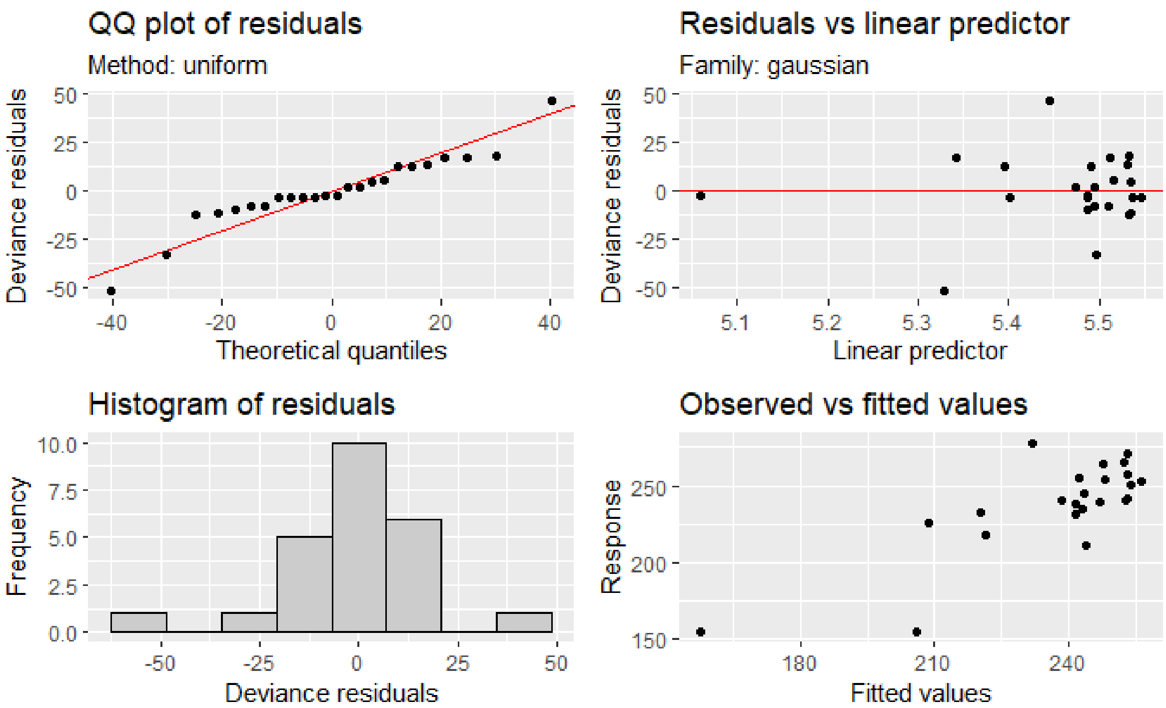
	df <dbl>	AIC <dbl>
lm	3	48251.91
poly2	4	48243.31



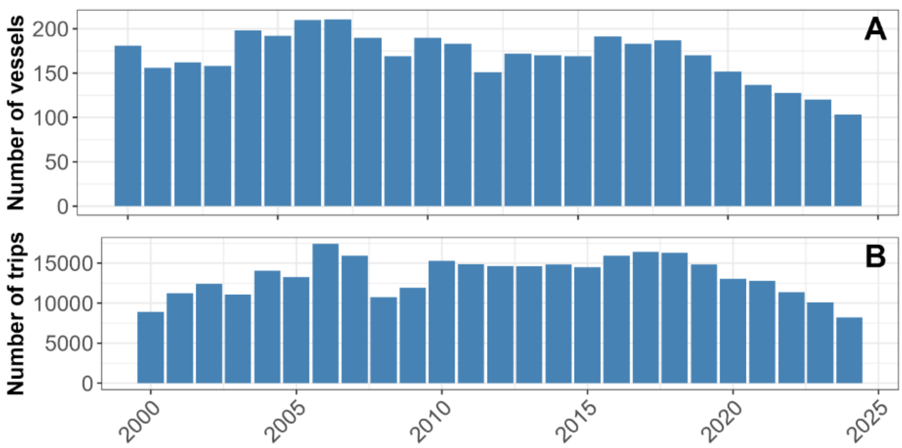
Appendix 13. *Model selection for detrended MHW detection*

	df	AIC
Model with presence summer MHWs + temp_summer (log(gauss))	6.18	220.48
Model without presence MHWs + temp_summer (log(gauss))	5.80	218.52
Model with presence MHWs + temp_summer (Gamma)	6.07	224.26
Model without presence MHWs + temp_summer (Gamma)	5.59	222.36
Model with presence MHWs + temp_summer (Tweedie)	7.13	224.44
Model without presence MHWs + temp_summer (Tweedie)	6.69	222.45
Model with presence MHWs + temp_summer + interaction(log(gauss))	6.18	220.48
Model with presence MHWs + temp_summer + interaction (Gamma)	6.07	224.26
Model with presence MHWs + temp_summer + interaction (Tweedie)	7.13	224.44

Appendix 14. *AIC of GAM models tested*



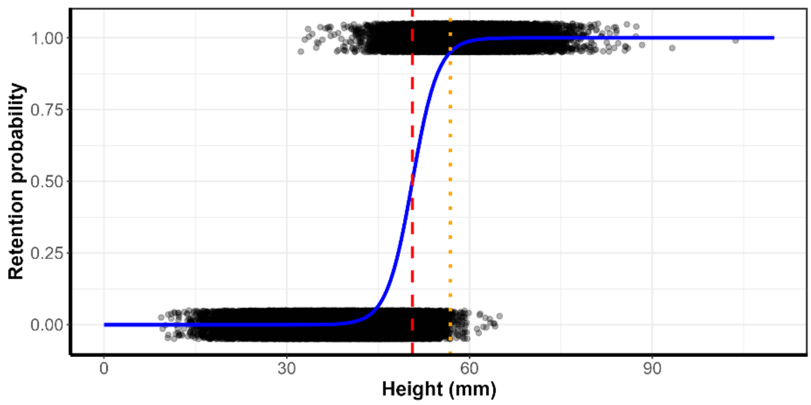
Appendix 15. *Diagnostic plot of the best GAM model (LPUEt ~ summer_tempt-1)*



Appendix 16. *Annual number of vessels (A) and fishing trips (B) landing whelks in the Western English Channel (2000–2025)*

***Appendix 17**. Measurement of shell width of a whelk. Photo credit: Author.*

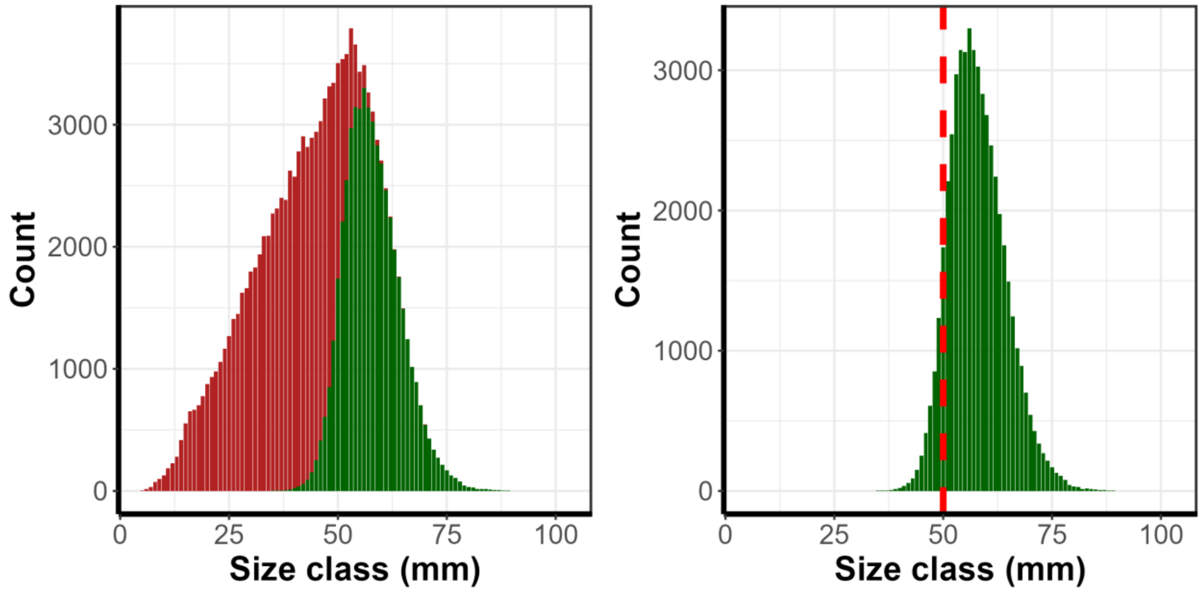
***Appendix 18.** Measurement of shell height of a whelk. Photo credit: Author.*



***Appendix 19.** Whelk Retention Curve in the Western English Channel (2021-2025), Sorting Grid 22 mm*

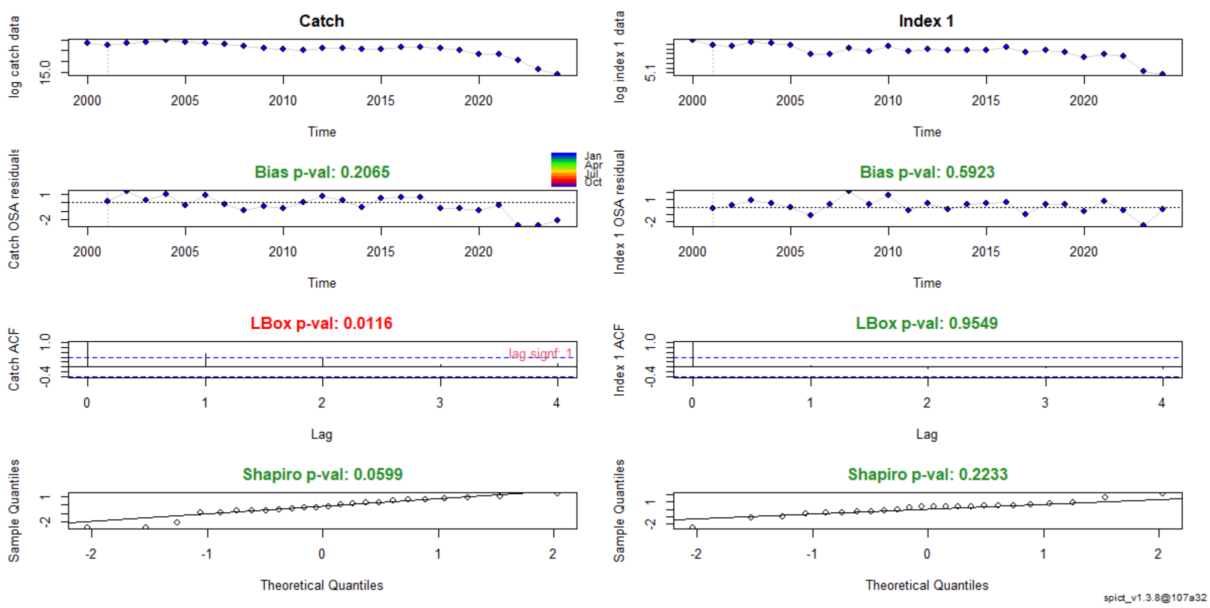
Retention probabilities were applied using a logistic model fitted to the selectivity of the sorting grid, in order to isolate only the commercial fraction of the landings (see appendix).

Regarding selectivity, which was estimated using the current regulatory sorting grid (22 mm) between 2021 and 2025, the results show a strong relationship between individual size and the probability of being retained by the grid (p-value < 2e-16). The SL_{50} (size at which 50% of individuals are retained) is estimated at 50.61 mm, while the SL_{95} is 56.82 mm.

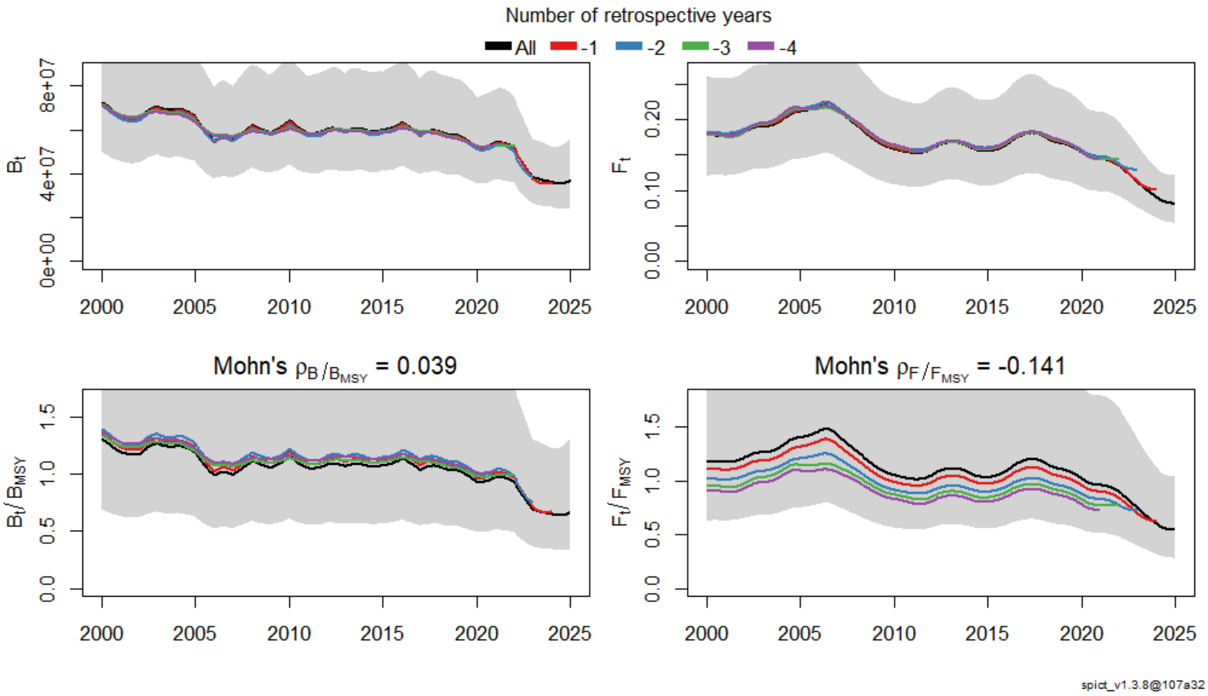


Appendix 20. *Size-frequency distribution of whelk before (left) and after (right) applying the retention selectivity of the sorting grid (Lc indicated by the red dashed line)*

According to ICES recommendations (2018), the length at first capture (Lc) is estimated here at 50 mm, corresponding to the size class where half of the maximum number of individuals is observed in the retained (commercial) fraction (see appendix). This Lc value is a key parameter used to calculate Lopt and the other length-based indicators.



Appendix 21. *OSA Residual Diagnostics from the SPiCT Model: Catch and Biomass Index*



Appendix 22. *SPiCT Retrospective Analysis - Diagnostics of Biomass and Fishing Mortality Estimates*

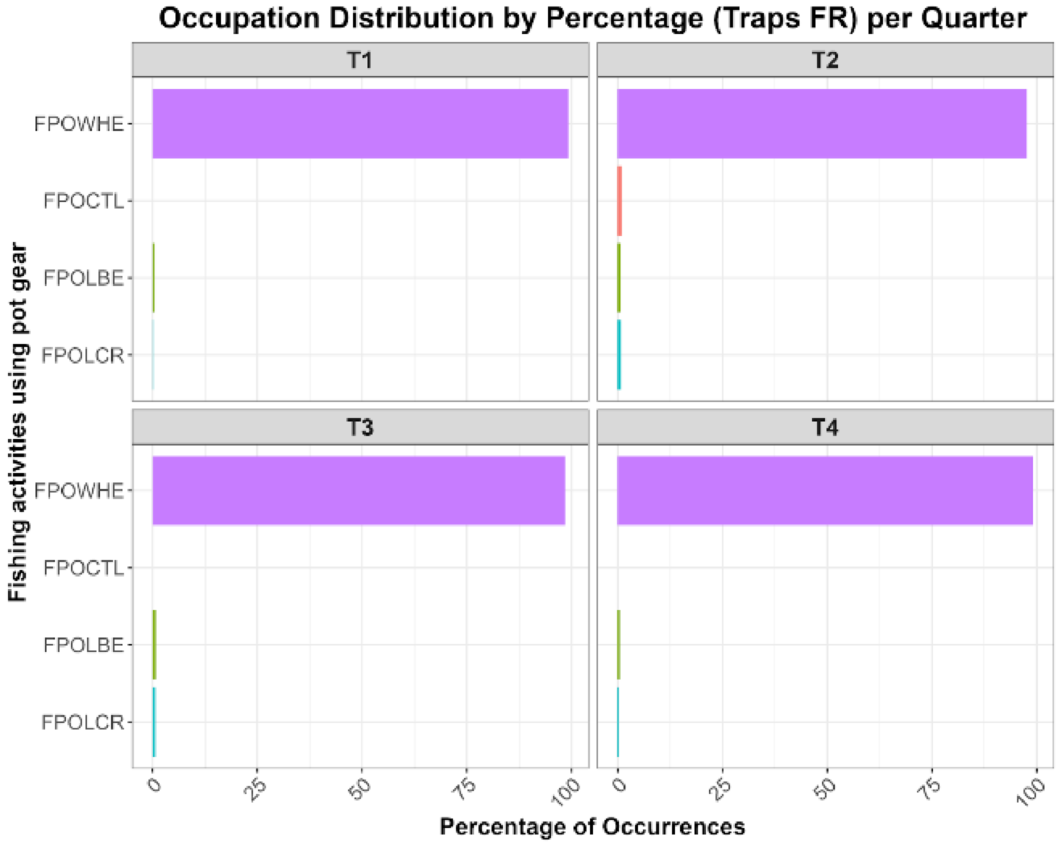
$resmat

	Distance	m	K	q	sdb	sdf	sdi	sdc
Basevec	0.00	8692150	113417350	0	0.1	0.1	0.02	0.01
Trial 1	13.96	8692153	113417364	0	0.1	0.1	0.02	0.01
Trial 2	1.69	8692151	113417351	0	0.1	0.1	0.02	0.01
Trial 3	5.57	8692151	113417344	0	0.1	0.1	0.02	0.01
Trial 4	14.10	8692150	113417336	0	0.1	0.1	0.02	0.01
Trial 5	5.64	8692151	113417344	0	0.1	0.1	0.02	0.01
Trial 6	80.90	8692153	113417431	0	0.1	0.1	0.02	0.01
Trial 7	19.55	8692151	113417330	0	0.1	0.1	0.02	0.01
Trial 8	10.55	8692149	113417339	0	0.1	0.1	0.02	0.01
Trial 9	22.52	8692152	113417372	0	0.1	0.1	0.02	0.01
Trial 10	35.01	8692153	113417385	0	0.1	0.1	0.02	0.01

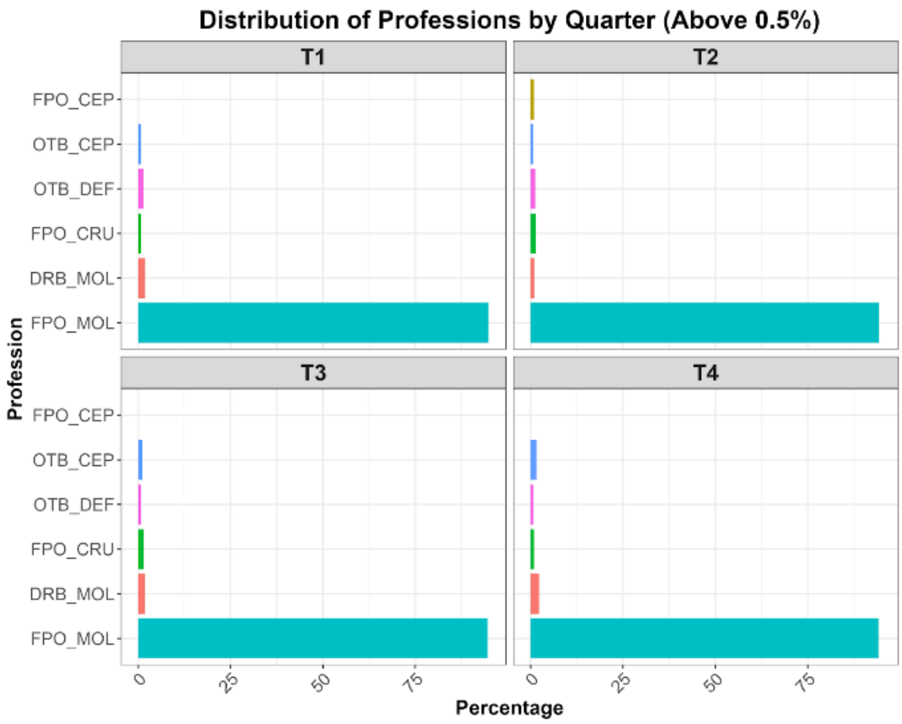
Appendix 23. *Stability analysis of parameter estimates in the SPiCT model based on resampling trials.*

```
Fixed parameters


Model parameter estimates w 95% CI
            estimate        cilow        ciupp    log.est
 alpha  1.681148e-01 2.728260e-02 1.035921e+00  -1.783108
 beta   1.202172e-01 2.076340e-02 6.960419e-01  -2.118455
 r      3.065545e-01 1.856552e-01 5.061838e-01  -1.182360
 rc     3.065545e-01 1.856552e-01 5.061838e-01  -1.182360
 rold   3.065545e-01 1.856552e-01 5.061838e-01  -1.182360
 m      8.692150e+06 6.655921e+06 1.135132e+07  15.977931
 K      1.134173e+08 6.757222e+07 1.903666e+08  18.546585
 q      4.400000e-06 3.100000e-06 6.400000e-06 -12.330093
 sdb    1.049320e-01 7.866540e-02 1.399690e-01  -2.254443
 sdf    1.048872e-01 7.502480e-02 1.466357e-01  -2.254870
 sdi    1.764060e-02 3.045500e-03 1.021823e-01  -4.037551
 sdc    1.260920e-02 2.205300e-03 7.209670e-02  -4.373325

Deterministic reference points (Drp)
           estimate        cilow        ciupp   log.est
 Bmsyd 5.670867e+07 3.378611e+07 9.518331e+07 17.853438
 Fmsyd 1.532773e-01 9.282760e-02 2.530919e-01 -1.875507
 MSYd  8.692150e+06 6.655921e+06 1.135132e+07 15.977931
Stochastic reference points (Srp)
           estimate        cilow        ciupp   log.est rel.diff.Drp
 Bmsys 5.551418e+07 3.319982e+07 9.282653e+07 17.832149  -0.02151693
 Fmsys 1.505435e-01 9.065740e-02 2.499890e-01 -1.893503  -0.01815925
 MSYs  8.354036e+06 6.374589e+06 1.094814e+07 15.938255  -0.04047317

States w 95% CI (inp$msytype: s)
                    estimate        cilow        ciupp    log.est
 B_2024.94      3.653298e+07 2.416166e+07 5.523872e+07 17.4137261
 F_2024.94      8.149540e-02 5.435130e-02 1.221960e-01 -2.5072081
 B_2024.94/Bmsy 6.580838e-01 3.336866e-01 1.297848e+00 -0.4184230
 F_2024.94/Fmsy 5.413414e-01 2.808387e-01 1.043483e+00 -0.6137052

Predictions w 95% CI (inp$msytype: s)
                  prediction        cilow        ciupp    log.est
 B_2026.00      4.127192e+07 2.617848e+07 6.506763e+07 17.5356929
 F_2026.00      8.149560e-02 5.159340e-02 1.287283e-01 -2.5072060
 B_2026.00/Bmsy 7.434482e-01 3.592593e-01 1.538486e+00 -0.2964562
 F_2026.00/Fmsy 5.413425e-01 2.716246e-01 1.078885e+00 -0.6137031
 Catch_2025.00  3.170025e+06 2.521622e+06 3.985158e+06 14.9692501
 E(B_inf)       7.857087e+07           NA           NA 18.1795116
```

***Appendix 24**. SPiCT Model Parameter Estimates, Reference Points, and Predictions*



Appendix 25. *Percentages of Occurrences of Metiers Using Pot Gear for Whelk Landings per Quarter (SACROIS, 2000-2024)*



Appendix 26. *Percentages of Occurrences of Metiers with Whelk Landings per Quarter Above 0.5% (SACROIS, 2000-2024)*

Appendix 27. *Morphometric Relationships of Whelk (Buccinum undatum) in the Western English Channel*

These morphometric data form a fundamental basis for describing the growth dynamics of the whelk stock in the WEC. They are particularly useful for predicting unmeasured traits (e.g., shell width or weight from height), for parameterizing selectivity models, and for improving the biological realism of stock assessment models.

Width-Height relationship

To characterise the relationship between shell height and shell width in whelks from the WEC, a linear regression model was fitted to individual-level data. The model follows the general form:

$$Wi = aH + b + \varepsilon$$

where:

- Wi is the width of the whelk (in mm),
- H is its shell height (in mm),
- a is the slope coefficient (variation in width per unit of height),

- b is the intercept,
- ε is the random error term, assumed to be normally distributed as $N(0, \sigma^2)$

The model fitting was performed using the lm() function in R software (R Core Team, 2025). This morphometric relationship is used to predict shell width from shell height, particularly in selectivity analyses based on size distributions.

Weight-Height relationship

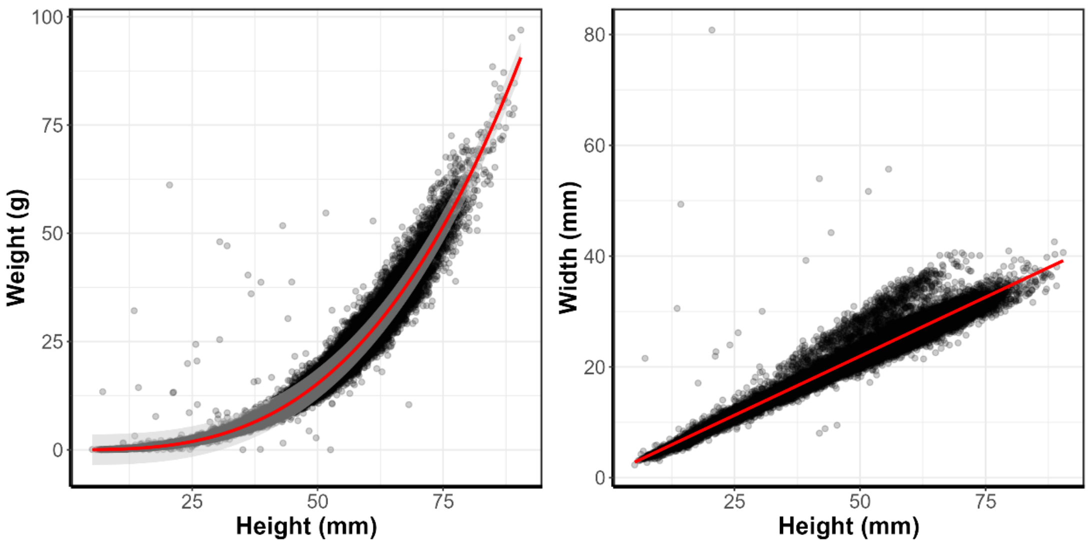
The relationship between weight (in g) and shell height (in mm) in whelks from the WEC was modelled using an allometric function of the form:

$$We = a*Hb + \varepsilon$$

where:

- We is the weight of the whelk (in g),
- H is its shell height (in mm),
- a is the scaling coefficient,
- b is the allometric exponent,
- ε is the random error term, assumed to be normally distributed as $N(0, \sigma^2)$

This non-linear model, which has a typical structure for biological mass-length relationships, assumes cubic growth when $b \approx 3$. The model was fitted using the nls() function in R (R Core Team, 2025), with initial parameter values set to $a = 0.01$ and $b = 3$, consistent with the assumption of isometric growth. The model was applied to the full dataset for which both weight and shell height were measured simultaneously, with the objective of predicting weight from shell height.



A27. *The relationship between weight (in g) and width (in mm) as a function of height (in mm).*

The linear model fitted on a total of 61,767 individuals reveals a significant relationship between shell height and width (p-value < 2e-16). The equation of the model is as follows:

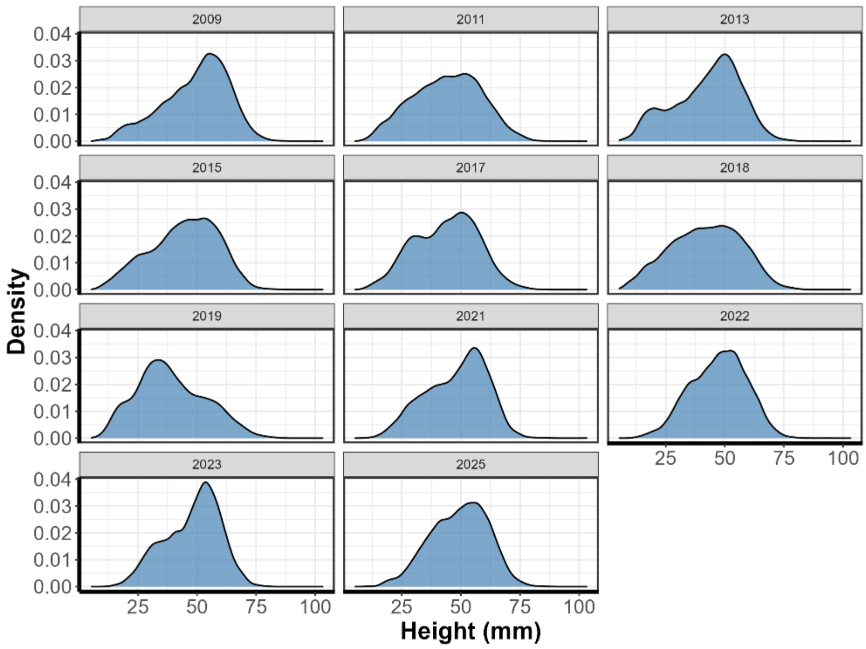
$$Wi = 0,62 + 0,43*H$$

Both model coefficients are significantly different from zero (p-value < 2e-16), indicating that shell height strongly contributes to the prediction of shell width. The slope coefficient (0.426) reflects an average increase of 0.426 mm in width for each additional millimeter of height. The model shows a high coefficient of determination (R^2 = 0.959), indicating that 95.9% of the variance in width is explained by height. The standard error of the residuals is estimated at 1.26 mm, indicating a good fit to the data.

The nonlinear weight-height relationship model was successfully fitted to a total of 74,935 individuals. The equation of the model is as follows:

$$We = 1,22\times10-4 * H3$$

Both estimated parameters are significant (p-value < 2e-16), reflecting a robust relationship between shell height and weight. The exponent b = 3.00 indicates a near-perfect cubic relationship between whelk height and weight, which is consistent with biological expectations for isometric growth in volume. The standard error of the residuals is estimated at 1.80 g, reflecting a precise fit of the model to the data.



***Appendix 28**. Distribution of height of whelk shells in the WEC by year*

The size structure of whelk in the WEC, observed between 2009 and 2025, shows a generally multi-modal distribution, reflecting the presence of several cohorts. A main mode between 50 and 60 mm is observed in most years. In 2019, the distribution differs, with a marked concentration around 30 mm.

Appendix 29. *Models of LPUE and environmental drivers across distributions*

Models tested	Family distribution
log(LPUE$_t$) ~ temp_summer $_{t-1}$	Gaussian
log(LPUE$_t$) ~ temp_summer $_{t-1}$	Gamma
log(LPUE$_t$) ~ temp_summer $_{t-1}$	Tweedie
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + temp_summer $_{t-1}$	Gaussian
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + temp_summer $_{t-1}$	Gamma
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + temp_summer $_{t-1}$	Tweedie
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + s(temp_summer $_{t-1}$) + ti(presence_MHWs$_{t-1}$, temp_summer $_{t-1}$)	Gaussian
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + s(temp_summer $_{t-1}$) + ti(presence_MHWs$_{t-1}$, temp_summer $_{t-1}$)	Gamma
log(LPUE$_t$) ~ presence_MHWs$_{t-1}$ + s(temp_summer $_{t-1}$) + ti(presence_MHWs$_{t-1}$, temp_summer $_{t-1}$)	Tweedie

L'INSTITUT agro Rennes Angers	Diplôme : Master Spécialité : SML-Biologie Spécialisation / option : Sciences Halieutiques et Aquacoles (EcolH) Enseignant référent : Etienne RIVOT

Auteur(s) : Yohan ANSEL Date de naissance* : 15/01/2000	Organisme d'accueil : Ifremer Adresse : Avenue Général De Gaulle, 14520 Port-en-Bessin Huppain Maître de stage : Hubert DU PONTAVICE
Nb pages : 35 Appendixe(s) : 29	
Année de soutenance : 2025	

Titre français : Contexte du changement climatique pour un stock à données limitées : le cas du bulot (*Buccinum undatum*) de Manche Ouest

Titre anglais : Climate Change Context of a Data-Limited Stock: The Case of Whelk (*Buccinum undatum*) in the Western English Channel

Résumé (1600 caractères maximum) : Des études montrent que le changement climatique, via le réchauffement océanique et les vagues de chaleur marines (MHWs), peut modifier la productivité des populations situées à la limite de leur aire. Pour les stocks à données limitées, ces impacts restent peu documentés. Nous analysons le cas du bulot (Buccinum undatum) de la Manche Ouest en croisant données halieutiques (VMS/AIS, débarquements, LPUE) et indices environnementaux (SST, MHWs). Nos résultats révèlent un réchauffement à long terme des habitats, des modifications des régimes saisonniers et une hausse de la fréquence des MHWs. La modélisation statistique montre qu'un dépassement estival des seuils thermiques de l'espèce, surtout lors de MHWs, est associé à une baisse d'abondance à court terme, tandis que des hivers doux pourraient affecter le recrutement avec décalage. Les approches d'évaluation adaptées aux stocks à données limitées (indicateurs de taille, SPiCT) indiquent un déclin de la biomasse et de la productivité, suggérant que les points de référence actuels sous-estiment l'influence du climat sur la dynamique du stock. Ces résultats appellent à intégrer les variables environnementales dans les évaluations et à adapter les stratégies de gestion pour garantir la durabilité des pêcheries côtières face au changement climatique.

Abstract (1600 caractères maximum): Studies have shown that climate change, through long-term ocean warming and marine heatwaves (MHWs), can affect the productivity of populations located at the edge of their distribution range. For data-limited stocks, however, the magnitude and mechanisms of these impacts remain poorly documented. We examine the case of whelk (Buccinum undatum) in the Western English Channel by combining fishery data (VMS/AIS, landings, LPUE) with environmental indicators (SST trends, MHW metrics). Results reveal long-term warming of whelk habitats, shifts in seasonal thermal regimes, and an increase in MHW frequency. Statistical modeling shows that summer temperatures exceeding species-specific thresholds, particularly during MHWs, are associated with short-term declines in abundance, while lagged effects of mild winters may influence recruitment. Assessment methods adapted to data-limited stocks (length-based indicators, SPiCT) indicate a decline in biomass and productivity, suggesting that current biological reference points may underestimate the influence of climate on stock dynamics. These findings highlight the need to integrate environmental variables into assessment frameworks and adapt management strategies to ensure the sustainability of coastal fisheries under climate change.

Mots-clés : Bulot, Manche Ouest, Changement climatique, Vagues de chaleur marines, LPUE, Stock limité en données, Conditions thermiques, Dynamique de population, Évaluation des stocks, Durabilité de la pêcherie

Key Words: Whelk, Western English Channel, Climate change, Marine heatwaves, LPUE, Data-limited stock, Thermal conditions, population dynamics, Stock assessment, fishery sustainability

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