Plankton and fish(eries) in pelagic habitats around the UK

PIT-PAF project report part B

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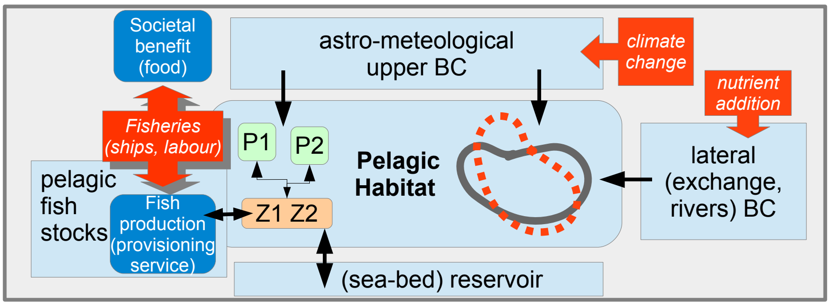
Abstract

This document reports an analysis of correlations between plankton indicators, derived from Continuous Plankton Recorder (CPR) data, and data for stocks of, and catches from, planktivorous fish, in selected pelagic habitats around the UK. These fish are herring, Norway pout, sprat and sandeels. The analysis focussed on annual statistics relating to (a) ICES statistical and 'traditional' CPR areas within the North Sea, and (b) selected examples of the COMP4 areas specified by OSPAR for the recent QSR. This spatiotemporal scale is larger than that which was the focus of part A of PIT-PAF (Thompson et al., 2024), and the main concern of this part B has been in 'top-down' relationships, viewing stocks of planktivorous fish as trophic boundary conditions on pelagic habitats, and pelagic fisheries as anthropogenic pressures on pelagic systems.

Although the plankton data indicated substantial change in abundances of some lifeforms and in the balance of organisms (as shown by use of the Plankton Index tool), few correlations between fish/fisheries and plankton were found. This could be because; some of the time-series used were too short; the spatial scale of assessment did not correspond to the scale on which interactions between populations of plankters and stocks of fish are evident; or, the North Sea ecosystems include complex feedback loops that overwhelm simple correlations.

Key messages

1. PELAGIC HABITAT FOOD WEBS: a *pelagic habitat* comprises the water column plus the plankton; feeding in these habitats are *planktivorous* fish such as herring, sprat, sandeel and pout for which zooplankters (Z) provide a key food supply, in turn dependent on production by, and balance of organisms in, the phytoplankton (P). The diagram includes various *boundary conditions* (BC) on pelagic habitats, and the 'bottom up' and 'top down' control perspectives, as well as the contributions these habitats make to ecosystem services.



2. LINKS BETWEEN PLANKTON AND FISH ARE SCALE DEPENDENT:

small scale of 100 m to 10 km and a few days, the scale of plankton patches, attracting fish shoals for feeding;

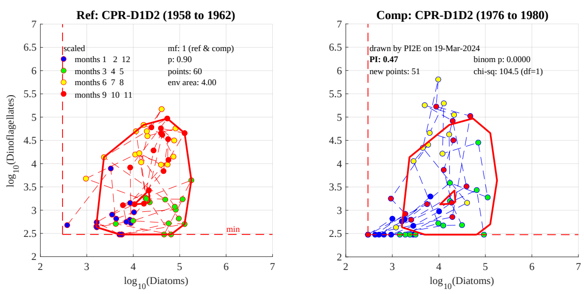
medium scale of 10 to 100 km and weeks-months, the scale on which local-area ecohydrodynamic factors control plankton type and condition, in turn influencing fish species and condition: **PIT-PAF part A**;

pelagic habitat assessment scale of 100 to 500 km and annualised statistics, ideally ~homogenous for seasonal cycle and types of plankton: **PIT-PAF part B - this study**;

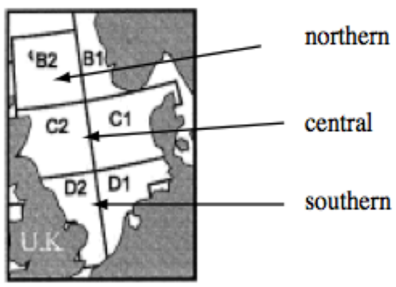
UK scale , that of the waters around our islands, within which fish migrate, and which is used for valuation of ecosystem services and natural capital.

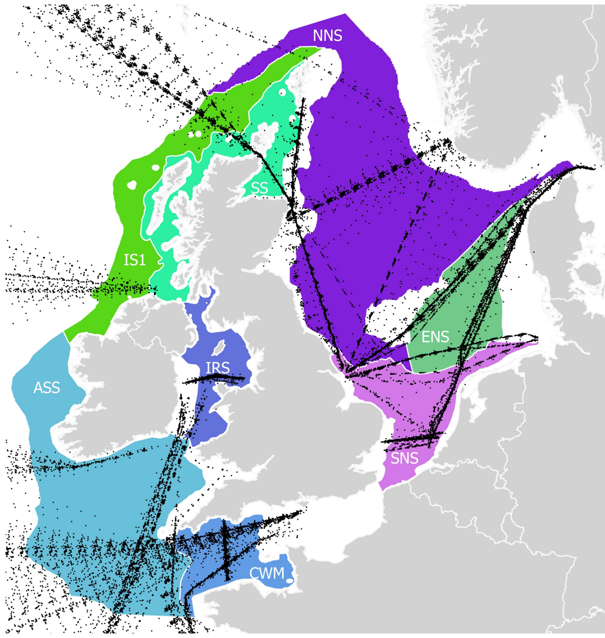
3. Planktonic LifeForms used as Indicators of the state of pelagic habitats. A *lifeform* is a group of plankters that respond in the same way to environmental conditions and play a similar part in food webs and biogeochemical cycling. Three pairs of lifeforms were used: diatoms and dinoflagellates; large and small copepods; and euphausiids and appendicularians. The pairs were used to construct time-series of values of the *Plankton Index* (PI) as an indicator of the *balance of organisms*.

PI diagram example. Monthly means were plotted to make a reference envelope (*left*), which was copied (*right*) so that new data could be plotted. The PI value was the proportion of new points within the envelope. For time-series, the comparison period was 1 year.

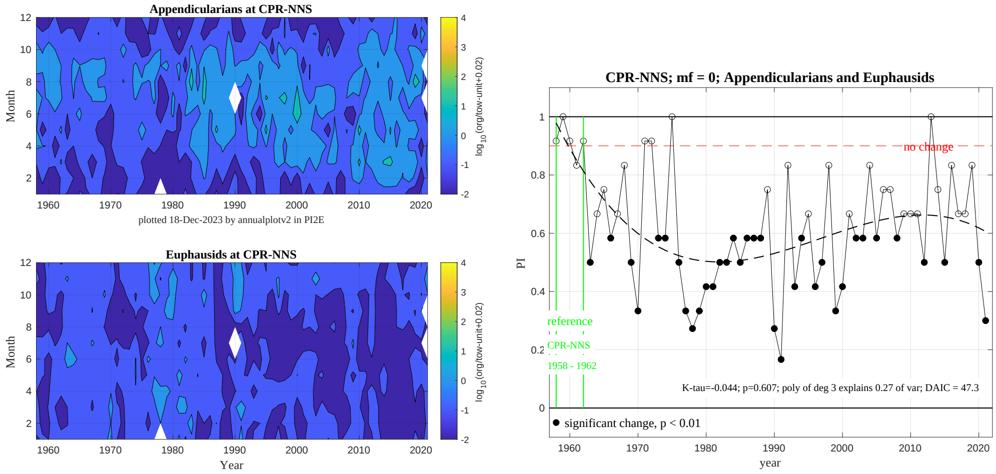


4. Pelagic Habitat Assessment Areas: two sets of areas were used: *left, below* the 'traditional' CPR subdivisions of the North Sea (roughly equivalent to ICES subdivisions); *right*, selected OSPAR COMP4 units: IRS, SS, NNS and SNS were used.



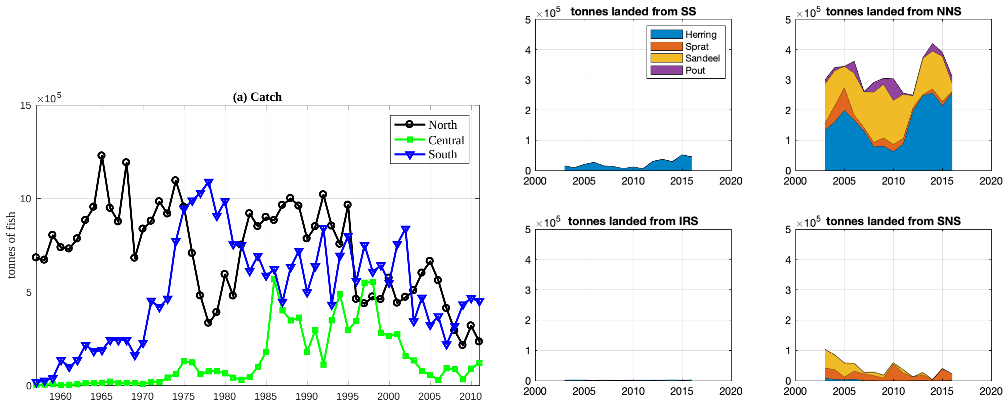


5. Lifeform abundances and Balance of Organisms are changing as shown in this example for the euphausiid-appendicularian pair, and the PI series derived from it, for the northern North Sea (NNS) COMP4 area.



There was significant change in 13 out of 24 instances (lifeforms × COMP4 areas) and significant PI trends in 8 out of 12 instances.

6. Fish and Fisheries time-series were constructed from data obtained from ICES, Cefas and STEFC. *Left* synthesised time-series for annual catch, totalled over herring, pout, sprat, and sandeel, for the three 'traditional' CPR subdivisions of the North Sea. *Right* stacked plots of landings for these four fish from catches in each COMP4 areas: highly spatially resolved data were only available from 2003. Timeseries were also made of planktivore biomass.



7. Correlation is weak: bivariate correlation was investigated for

   - total planktivore biomass (TPB) and catch, for the three CPR traditional areas and the diatom-dinoflagellate PI: out of 6 possible correlations, only one was significant: *catch and diatom-dinoflagellate PI for the south area of the North Sea, 1958-2010*;
   - planktivore biomass, and forage fish Landings, for the four COMP4 areas and the PI series for the three pairs of lifeforms: out of 24 possible correlations, only one was significant: *landings and large-copepod-small-copepod PI in the COMP4 Scottish Sea, 2003-2016.*

8. Conclusions

   - The plankton data indicated substantial change in abundances of life-forms and in the balance of organisms;
   - Few correlations between fish/fisheries and plankton were found. This could be because; some of the time-series used were too short; the spatiotemporal scale of assessment did not correspond to the main scale on which stocks of fish interact with populations of plankters; the surveyed marine ecosystems include complex feedback loops conferring resilience against changes in pressures; or, fishing might not be the main pressure on the pelagic system.
   - Given the change in the balance of organisms, which might lead to a *regime shift* with consequences for ecosystem services, it is essential to continue to monitor the state of pelagic habitats and to explore new ways of linking them to fisheries.

Contents

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1 Introduction

The marine ecosystems in the UK's territorial and shared waters represent *natural capital assets* that supply *ecosystem services* to UK society. Ecosystems "combine the abiotic environment with biological communities . . . [in] self-organising, regenerative functional units [made up of] combinations of life-forms that control such fluxes as [those] of energy . . . nutrients . . . , and organic matter " (Dasgupta, 2021). One important ecosystem service is that of *provisioning*, in the present case that of providing stocks of fish available for capture by fisheries. This service relies on fluxes of organic matter through food webs such as that reproduced in Figure 1.

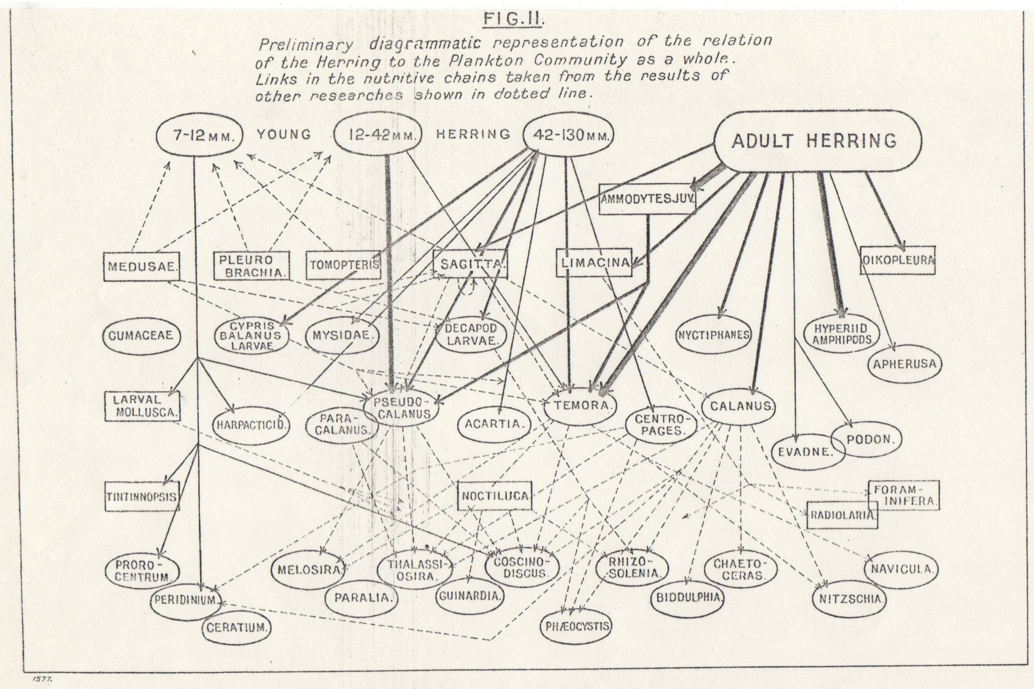

Figure 1: The food web of the herring (Hardy, 1924).

Marine ecosystems consist of pelagic and benthic habitats and the mobile animals, such as fish, that use these habitats (Cochrane et al., 2010). A *pelagic habitat* comprises the drifting organisms of the plankton, and the physico-chemical environment of the water column, within a part of the sea in which *ecohydrodynamic conditions* can be considered homogenous. The immediate predators on the plankton are *planktivorous* fish such as herring, sprat, sandeel and pout, as confirmed by examination of the stomach contents of these fish (Thompson et al., 2022).

Hardy (1924) extended his food-web diagram to the phytoplankters on which zooplankters feed, thus bringing in the photosynthetically-driven primary production on which most food-webs depend. The result is a complex pattern of links, which should, furthermore, be understood as changing in time and space. Consequently, the search for evidence of relationships between plankton and fish is not straightforward, and can lead to different results, depending on the space and time scales (Table 1) on which the relationships are sought.

Understanding these relationships is important not only for managing the ecosystem provisioning service that supports fisheries but also for understanding the impact of fishing, alongside other human activities, on the health of the pelagic habitats. Thus motivated, the PIT-PAF project has investigated two of the scales in the Table. This report describes part B, dealing with relationships between annualised indicators on the scale called *pelagic habitat (PH) units* in the Table, units exemplified by the COMP4 sea-areas identified by OSPAR for its 2023 Quality Status Report (e.g. Holland et al., 2023a).

Table 1: Scales on which fish and plankton interact. A *pelagic habitat* (PH) comprises plankton and water-column. *Ecohydrodynamic* refers to the ecologically-relevant features of the latter, such as stratification.

space scale	time scale	relevant characteristics of features on this scale
small: 100 m to 10 km	days	plankton patches, attracting fish shoals for feeding; correlation might be + or - ve, depending on sampling relative to formation of patch and arrival of fish
medium: 10 to 100 km	weeks-months	local/ temporary ecohydrodynamic factors controlling plankton type and condition, in turn influencing fish species and condition: PIT-PAF **part A**
PH units: 100 to 500 km	annual	pelagic habitat assessment units that are assumed ∼homogenous for seasonal cycle and types of plankton; PIT-PAF **part B**; some fish stocks, e.g. sandeel, localised on this scale
UK: 1000 km	annual +	ICES main areas for fisheries science; UK territorial and associated waters; the lifecycle of e.g. the North Sea herring takes place on this scale and involves several PH units

2 Conceptual framework

The acronym PIT-PAF stands for *Putting It Together - Plankton and Fisheries*, and the general aim of the project was to explore statistical links between plankton and fish from these two perspectives:

- **fisheries science**: *what ecosystem variables control abundance and condition of fish for fisheries?*
- **pelagic ecology**: *what pressures, including pelagic fisheries, act on the pelagic habitat and the plankton?*

The fisheries perspective is 'bottom-up', being interested in the way primary production flows 'upwards' through the food-web, providing an *intermediate ecosystem service* in the terms of the UK Millennium Ecosystem Assessment (Turner et al., 2015), and the way that changes in the balance of planktonic lifeforms might impact on fish stocks. Several studies (Heath, 2005b,a; Frederiksen et al., 2006; Capuzzo et al., 2018) have provided evidence for such 'bottom-up' control of pelagic food webs in the North Sea.

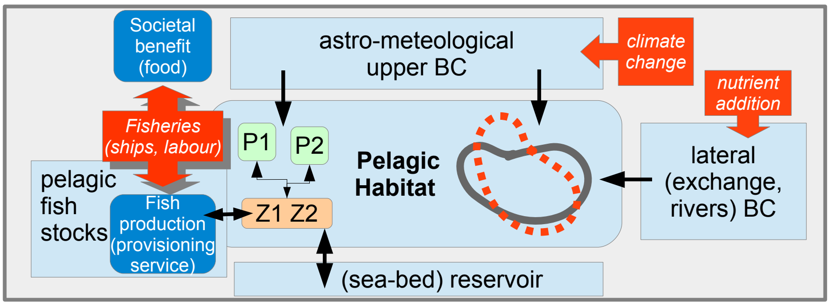

Figure 2: Conceptual model of the relationship between plankton and fisheries. Large arrows show boundary conditions (BC). i.e. fluxes of energy, freshwater, nutrients or biomass; small arrows show more complex causal links, either 'top down' or 'bottom up. The *pelagic habitats* comprise plankton and their water-column environment; the *pelagic system* includes the planktivore fish, which are harvested commercially by pelagic fisheries. BENTHOS

In contrast, the pelagic ecology perspective is 'top-down', viewing consumption of plankton by fish as a trophic *boundary condition* on the biological system in pelagic habitats, potentially able to influence the balance of organisms amongst plankters. Fewer studies have adopted this perspective.

Additionally, the human impact on such consumption, by way of harvesting of planktivore fish by commercial fisheries, can be understood, in terms of the DPSIR conceptual framework (Luiten, 1999), as a PRESSURE acting on the STATE of pelagic habitats. The terms PRESSURE and STATE are, here, capitalised to reference their meanings within the DPSIR framework, and also because it is useful to distinguish a system's climatological STATE, which in the case of pelagic habitats, includes seasonal variation, from a near-instantaneous *state*, such as that of a pelagic habitat during a particular month.

The 'top-down' and 'bottom-up' perspectives can be further distinguished by the following diagram:

$$\begin{array}{ccccccc} W & \dashleftarrow & \mathbb{E} & \mathbb{P} & \dashrightarrow & P & \\ & & \Uparrow & \Downarrow & & \downarrow & \text{implies } \updownarrow \\ & & & \mathbb{S} & \dashrightarrow & S & \end{array}$$

In this diagram, the right-hand side correspond to a DPSIR and 'top-down' perspective; the left hand side corresponds to a 'bottom-up' and ecosystem services perspective. P, S and W refer to indicators, which are human constructs; $\mathbb{E}, \mathbb{P}$ and $\mathbb{S}$ refer to things in the 'real' or biophysical world. P, $\mathbb{P}$ reference PRESSURE, while S, $\mathbb{S}$ reference STATE. $\mathbb{E}$ are the biophysical services provided by the pelagic system, and W is the human welfare or societal benefit generated by them.[1] The arrows $\Uparrow$ and $\Downarrow$ refer to 'real' causal connections, that between $\mathbb{P}$ and $\mathbb{S}$ implying, at least, the complex set of links shown in Figure 1, if not the myriad of interactions amongst plankters that can be aggregated on the scales in Table 1. The $\dashrightarrow$ and $\dashleftarrow$ represent the information flows that quantify indicators.

Of the two arrows between P and S, the $\updownarrow$ refers to *correlation* and the $\downarrow$ to a *mapping*, for example to an algorithm that allows ΔS to be predicted from ΔP. Ideally, such a mapping would be a mathematical representation of a mechanistic model that captures the key features, in aggregate, of the 'real' causal interactions between $\mathbb{P}$ and $\mathbb{S}$. Logic implies that, because it is known that the relationship $\mathbb{P} \Rightarrow \mathbb{S}$ exists and can be approximated by $P \rightarrow S$, there must be a correlation $P \leftrightarrow S$.This, of course, is the opposite of the usual epistemological problem, which concerns the induction of 'real' causal links from observed correlations. The **research question** addressed here concerns the search for such correlations on the spatio-temporal scales investigated during the present study, and also the adequacy of available data-sets, and indicator construction rules, to reliably capture in P and S the real changes in $\mathbb{P}$ and $\mathbb{S}$.

Figure 2 presents the 'real-world' issues graphically. The loops within the pelagic habit box refer to the mathematical *attractors* supposed to control seasonal cycles of the balance of planktonic organisms.

[1] 'Welfare' is here viewed as an indicator of the provisioning ecosystem service.

3 Pelagic Habitat assessment areas

This study has considered plankton-fish links on the spatiotemporal scale identified as areas suitable for assessment of the health of the pelagic habitats around the UK. It has proven challenging to identify such areas either in principle or practice (Graves et al., 2023), not to mention reconciling them with accounting units for ecosystem services and natural capital, and with the areas used for reporting fisheries statistics. What might be called a 'traditional' approach is that in Table 2, which lists the ICES Statistical Areas used for many years for fisheries statistics in the North Sea, and the roughly equivalent subdivisions used by the Continuous Plankton Recorder (CPR) survey. The CPR areas are illustrated in Figure 3.

Table 2: 'Traditional' subdivisions of the North Sea used by the Continuous Plankton Recorder (CPR) Survey and ICES. The two sets are presented as roughly equivalent. The easterly and westerly CPR areas are separated at 3°E. Extents estimated by the authors. ICES statistical areas from gis.ices.dk and Heath and Beare (2008). ICES 3a is the Skagerrak and Kattegat.

Area	**North**	**Central**	**South**
Main ecohydrodynamic types (Rodhe et al., 2006)	*seasonally or permanently stratified water-columns*		*permanently mixed water-columns and complex types*
Nutrient levels (Rodhe et al., 2006)	*Atlantic-influenced*	*lowest*	*anthropogenically enriched*
CPR area	**B1 B2**	**C1 C2**	**D1 D2**
latitude limits	58° to 63°N (B1) or 61°N (B2)	55° to 58°N	51° to 55°N
western limit	Britain & 3°W	Britain	Britain
eastern limit	Norway	Denmark & 8°E	Europe
extent c. 000 km^2	174	232	183
ICES statistical area	IVa or 4a	IVb or 4b	IVc or 4c
latitude limits	57.5° to 62°N	53.5° to 57.5°N	51° to 53.5°N
western limit	Britain & 4°W	Britain	Britain
eastern limit	3a & Norway	Europe & 3a	Europe
extent c. 000 km^2	202 (shelf only)	288	80

For recent assessments of pelagic habitat health, the UK has adopted a typology and mapping based originally on the physical characteristics of different parts of the seas of north-western Europe (van Leeuwen et al., 2015; McQuatters-Gollop et al., 2019) and recently modified by the OSPAR community (Blauw et al., 2019) by taking account not only of seasonal patterns of water-column stratification but also of remotely sensed patterns of ocean colour. The result is the COMP4 areas shown in Figure 3, which have been used for assessment of changes in pelagic habitats in the OSPAR 2023 QSR (Holland et al., 2023a). Tett et al. (2024) has proposed that these areas could also be used for identification of natural capital assets as spatial areas of specific ecosystem types, as required by the UK Principles of Natural Capital Accounting (ONS, 2017, 2023) and the UN System of Environmental-Economic Accounting (UN, 2021).

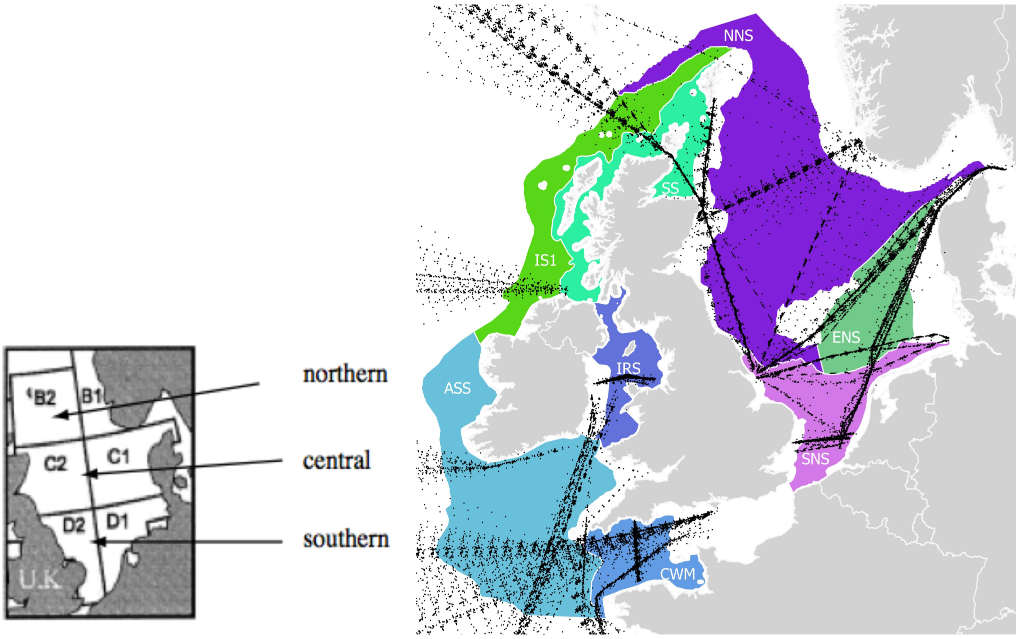

Figure 3: *Left*: 'Traditional' subdivisions of the North Sea for analysis of CPR data (e.g. Reid et al., 1990). *Right*: Selected OSPAR COMP4 areas (REF), showing CPR routes since 2000 (SOURCE). The four areas used in the present study were: SS (Scottish Sea); IRS (Irish Sea); NNS (Northern North Sea); and SNS (Southern North Sea). ???? provides shapefiles for the OSPAR COMP4 areas.

This report deals with both the 'traditional' CPR and the OSPAR COMP4 areas. Although the latter are more precisely related to pelagic habitat ecohydrodynamics, the former might be better for fisheries statistics.

4 Plankton

4.1 Continuous Plankton Recorder

Starting in the 1930s and continuing post-War, the Continuous Plankton Recorder (CPR) has been regularly towed by ships of opportunity along routes radiating from Britain (figure 3) and elsewhere. The instrument and methods of use and sample analysis were described by (Richardson et al., 2006) and have been largely unchanged since 1958. Water from a depth of about 7 metres enters the CPR and is filtered on a continuously moving mesh which traps plankton before winding on into a tank of preservative. The mesh from each tow is cut into sections (hereafter called *samples*) representing about 10 nautical miles towed or about 3 m^3 of water filtered (hereafter called a *tow unit*), and the preserved organisms subsequently identified and counted by specialists. Methods for phytoplankters differ from those for zooplankters. The latter are identified and counted on the whole of a sample section. The former are examined in 20 microscope fields along two diagonals of the sample, and taxon presence/absence records converted to cell numbers per sample. Arising from this are the challenges of data with a small dynamic range and containing many zero values, which, however, are ameliorated when sample data are averaged over a month and within a substantial sea-area (Tett and Bresnan, 2018). Compared with other sampling methods, the CPR underestimates abundances, more so for smaller organisms. Nevertheless, the survey provides consistent data over many decades.

4.2 Lifeforms

There are two contrasting approaches to understanding how the many species that can be identified in CPR samples contribute to the functioning of the pelagic habitats. They relate to *numerical biodiversity* and in *functional diversity*. The first uses indicators based on species richness and relative abundance (e.g. OSPAR PH3, Rombouts et al., 2019). The second, that of OSPAR PH1 indicators (Budria et al., 2017), requires identification of groups of species (not necessarily taxonomically related) that are similar in their roles within ecosystems (McQuatters-Gollop et al., 2019). Dasgupta (2021) saw adequate functional diversity, rather than species diversity, as key for healthy ecosystems, Terms such as functional group, or guild, have been proposed for these sets of species. PHEG uses the term **lifeform**, defined operationally for plankters as

- the set of traits that identifies a functional group within the plankton,

> thus a set of low-level taxa[2] (observed to possess these traits) that are supposed to respond in similar ways to ecohydrodynamic conditions and which are similar in their biogeochemical and trophic functions and interactions.

This use derives from Margalef (1978) (see also Wyatt, 2014), who saw lifeforms as traits related to survival in specific hydrodynamic conditions, and distinguished diatoms and dinoflagellates on this basis. Lifeform aggregation is also practically useful because it simplifies the number of variables to be considered when describing pelagic habitat STATE. Up to 6 lifeforms are used here (Table 3). Four are a subset of the set currently used for pelagic habitat assessment(McQuatters-Gollop et al., 2019; Holland et al., 2023a). Two (euphausiids and appendicularians) are additional, introduced because of their significance in relation to changes in food webs.

4.3 Plankton Index

The label Plankton Index (PI) refers to three things: (1) a set of concepts; (2) a software tool that implements those concepts for evaluating change in the condition of the pelagic habitats; and (3) one or more values output by the tool. There are two key concepts: first, that the STATE of the plankton can be adequately described by abundances of a set of *lifeforms*; and, second, that, given the strong seasonal patterns evident in temperate-water planktons, the *state* can be visualised by plotting regular (usually monthly) abundances of lifeforms in a *state space* defined by orthogonal axes of these abundances. Change in STATE appears as a movement of clouds of points out of an envelope drawn around a reference set of points. Although the method applies in principle to state spaces of any number of dimensions, in practice it is applied to pairs of lifeforms, as exemplified in Figure 4.

The tool was initially proposed to detect the *Undesirable Disturbance* associated with Eutrophication (Tett et al., 2007) and first implemented as the 'Phytoplankton Community Index' (Tett et al., 2008) to quantify the (transitional or coastal water) phytoplankton biological quality element of Annex V of the Water Framework Directive (WFD). It has been used subsequently in various contexts (e.g. Brito et al., 2015; Gowen et al., 2015; Mak et al., 2024). For purposes initially relating to the EU Marine Strategy Framework Directive and subsequently to the UK Marine Strategy and UK obligations to OSPAR, it was adapted to use with zooplankton as well as phytoplankton, and renamed the 'Plankton Index' (PI); however, difficulties in identifying a

[2] 'Low level taxa' refers to the lowest taxonomic level that have been reliably identified; this is ideally but not always species.

Table 3: Lifeforms used with CPR data. Those marked with † are not part of current standard set used by PHEG (McQuatters-Gollop et al., 2019).

Lifeform	short	Description
phytoplankton		*phytoplankters typically reproduce by cell division every few days during growth season*
(Pelagic) Diatoms	(P)DIA	Diatoms (*Bacillariophyceae*, example *Chaetoceros*), mostly microplanktonic in size, often chain-forming; excluding thick-walled species likely to have been resuspended from the seabed;
Dinoflagellates	DINO	'armoured' Dinoflagellates (*Dinophyceae*, example: *Ceratium*), mostly microplanktonic in size and able to swim a few metres vertically; regarded as a phytoplanktonic lifeform, even though including heterotrophs as well as myxotrophs; 'naked' forms don't survive contact with the CPR mesh;
zooplankton		*zooplankters typically reproduce sexually by egg-laying, with one or several generations per year*
Small Copepods	SCOP	pelagic crustaceans of class *Copepoda* that are less than 2 mm long as adults; example: *Acartia*
Large Copepods	LCOP	pelagic crustaceans of class *Copepoda* that are longer than 2 mm as adults; some migrate into deep water to over-winter; example: *Calanus*
Euphausiids†	EUPH	pelagic crustaceans of Malacostracan order *Euphausiacea*, adults 1-3 cm in length; over-winter in deep water; example: *Meganyctiphanes*
Appendicularians†	APPEND	pelagic tunicates of class *Appendicularia*, tadpole-like animals ($< 1mm$) that construct gelatinous floating houses within which to catch nanophytoplankton; example: *Oikopleura*

reference condition for 'Good Environmental Status' (GES) led to the idea of using values to track change relative to an arbitrary temporal reference condition, and seeking correlations with Pressures in order to identify deviations from GES (McQuatters-Gollop et al., 2019).

The plankton results presented in this document used version `PI2E` of SAMS Matlab coding of the PI tool. In addition to making PI diagrams and time-series of PI values, the program includes options for contour plots and for annual means of life-form abundances with interpolation of missing values. The program expects data pre-aggregated into lifeform abundances by assessment regions, but includes an option for averaging over a month if the data, for example, derive from individual CPR samples. Most averaging and display transforms lifeform abundances x with $\log_{10}(x + z)$, where z relates to the non-zero minimum of the x set.

4.4 Methods and Results: CPR areas, 1958 – 2010

This part of the analysis was begun in 2011 to examine relationships between PI time-series and PRESSURES in the North Sea. Because the main interest at that time was in the 'undesirable disturbance' that eutrophication might cause to the balance of organisms in the phytoplankton, the only lifeforms investigated were diatoms and dinoflagellates. CPR data for total diatoms and total dinoflagellates were supplied by SAHFOS (now MBA), in the form of lifeform totals for individual samples allocated to the traditional CPR areas. The lifeform aggregation was based on Richardson et al. (2006, table 5). These data had earlier been used to examine issues concerning zeros and low dynamic range in the CPR data (Tett and Bresnan, 2018), and possible artefacts resulting from changes of CPR towing routes around 1980 (Tett, 2016). For the present study they were input to the program `PI2E`, which carried out month-averaging.

Results are summarised in Table 4 and exemplified in Figure 4 for the 'North' area. All PI series showed a pattern of maximum deviation and then return towards the reference condition; the greatest deviations were seen around or just before 1980 in the 'South' and 'Central' areas.

4.5 Methods and Results: COMP4 areas, 1958 – 2021

Developments during the last decade have improved the scientific basis for delineating assessment areas for the pelagic habitats, with the recently identified COMP4 areas appearing to provide the best current basis for "linking offshore plankton communities to large-scale drivers of change such as climate warming" (Graves et al., 2023), and being used for the pelagic habitats

Table 4: Significant trends in life-form abundances and PI values in each traditional CPR area between 1958 and 2010. Monotonic trends in annual means of lifeform abundances were identified using the Mann-Kendall test, and curvilinear trends in the PI series were identified with least-squares fit of order-3 polynomials. Significant ($p \leq 0.01$) trends in lifeforms shown by $\Uparrow$ (increase) and $\Downarrow$ (decrease). $\cap\!\!\!\!\cup$ indicates a significant trend in the PI for the lifeform pair, explaining ≥ 0.28 of the variance in the time-series.

CPR	Lifeform	LF trend	PI trend
North	DIA	$\Uparrow$	$\cap$
	DINO		$\cup$
Central	DIA		$\cap$
	DINO	$\Downarrow$	$\cup$
South	DIA		$\cap$
	DINO	$\Downarrow$	$\cup$

in the most recent OSPAR QSR (Holland et al., 2023a).

Using shapefiles obtained from OSPAR, MBA-provided data from the CPR survey was filtered for the four COMP4 areas selected for study, chosen on the grounds that they exemplified conditions in different parts of UK and associated waters, and that they were adequately crossed by CPR routes. Next, abundances for low-level taxa were aggregated into the abundances per sample of each of the lifeforms in Table 3, using the most recent version of the UK Lifeforms 'Master List' REF for the standard lifeforms, and taxonomic assignment for euphausiids. 'Appendicularia' was already a unit. CHECK. Finally, these abundances were averaged by month, and the resulting data were input to the program `PI2E`, with results as follows.

Trends in the 6 lifeforms are shown, as contours of abundance on month-year surfaces, in figures 5 and 6. Of special interest was the trend of increase in Appendicularians, which was significant in all four COMP4 areas (Table 5). In contrast, Euphausiids, the other member of the life-form pair, decreased in three areas. The change in SNS was not significant, perhaps because euphausiid numbers were in low here, the shallow, turbid, mixed waters being unsuitable for this type of crustacean. Dinoflagellates also decreased significantly in all areas, whereas there was significant change (an increase) in Pelagic Diatoms, the other member of the life-form pair, only in SNS.

In the case of PI time-series (Figure 7), significant trends were apparent for all life-form pairs in NNS and SNS, but not in SS, and only weakly in IRS.

Table 5: Significant trends in life-form abundances and PI values in each COMP4 area. Monotonic trends in annual means of lifeform abundances were identified using the Mann-Kendall test, and curvilinear trends in the PI series were identified with least-squares fit of order-3 polynomials. Significant trends in lifeforms shown by $\Uparrow$ (increase) and $\Downarrow$ (decrease). $^{\cap}_{\cup}$ indicates a significant trend in the PI for the lifeform pair. Size (000 km^2) of areas from Graves et al. (2023).

COMP4	(size)	start	Lifeform	LF trend	PI trend
IRS	(33)	1971	APPEND	$\Uparrow$	$\cap$
			EUPH	$\Downarrow$	$\cup$
			LCOP		
			SCOP		
			PDIA		$\cap$
			DINO	$\Downarrow$	$\cup$
SS	(53)	1958	APPEND	$\Uparrow$	
			EUPH	$\Downarrow$	
			LCOP	$\Downarrow$	
			SCOP		
			PDIA		
			DINO	$\Downarrow$	
NNS	(265)	1958	APPEND	$\Uparrow$	$\cap$
			EUPH	$\Downarrow$	$\cup$
			LCOP		$\cap$
			SCOP		$\cup$
			PDIA		$\cap$
			DINO	$\Downarrow$	$\cup$
SNS	(62)	1958	APPEND	$\Uparrow$	$\cap$
			EUPH		$\cup$
			LCOP		$\cap$
			SCOP		$\cup$
			PDIA	$\Uparrow$	$\cap$
			DINO	$\Downarrow$	$\cup$

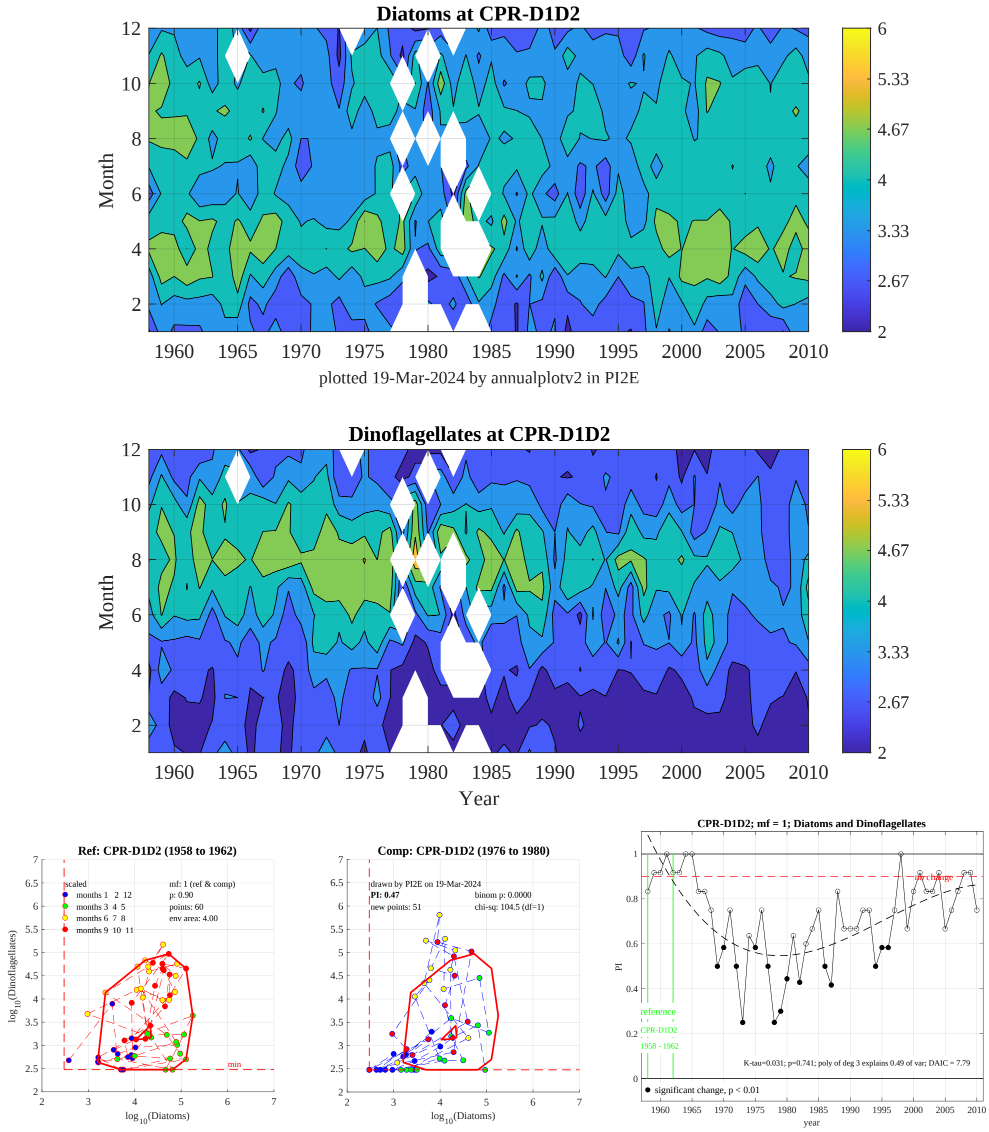

Figure 4: Example of the Plankton Index for CPR Diatoms and Dinoflagellates from the traditional CPR 'South' area of the North Sea, 1958 - 2010. *Top*: log-transformed lifeform abundances (per tow unit) contoured on a year-month surface. *Bottom left*: An example PI diagram, in which each plotted point is a monthly value, coloured by season. The left-hand part shows the reference envelope as a doughnut drawn to includes 90% of points. In the right-hand diagram, the PI value is the proportion of points from 1976–1980 that fall within the reference envelope: in this case 0.47, a significant change in the balance of organisms. *Bottom right*: the time-series of annual PI values (computed by comparing each year with the 5-year reference period), with fitted 3rd-order polynomial that explains a significant fraction (49%) of the variance. The PI is robust against missing data, such as that lost due to changes in CPR routes c. 1980.

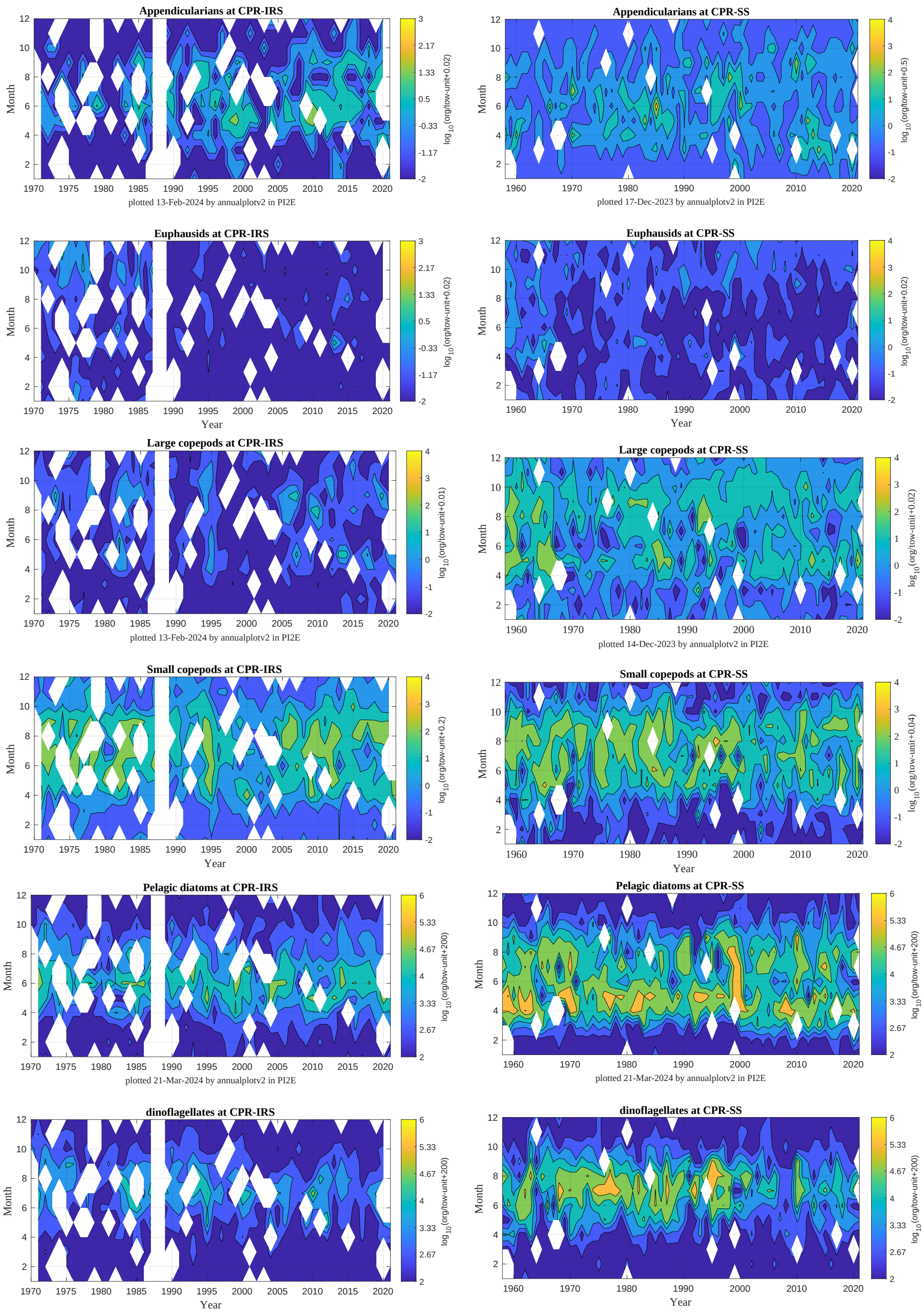

Figure 5: Lifeform contour plots for COMP4 areas: *left*, Irish Sea (where regular sampling commenced in 1971); *right* Scottish Sea (from 1958).

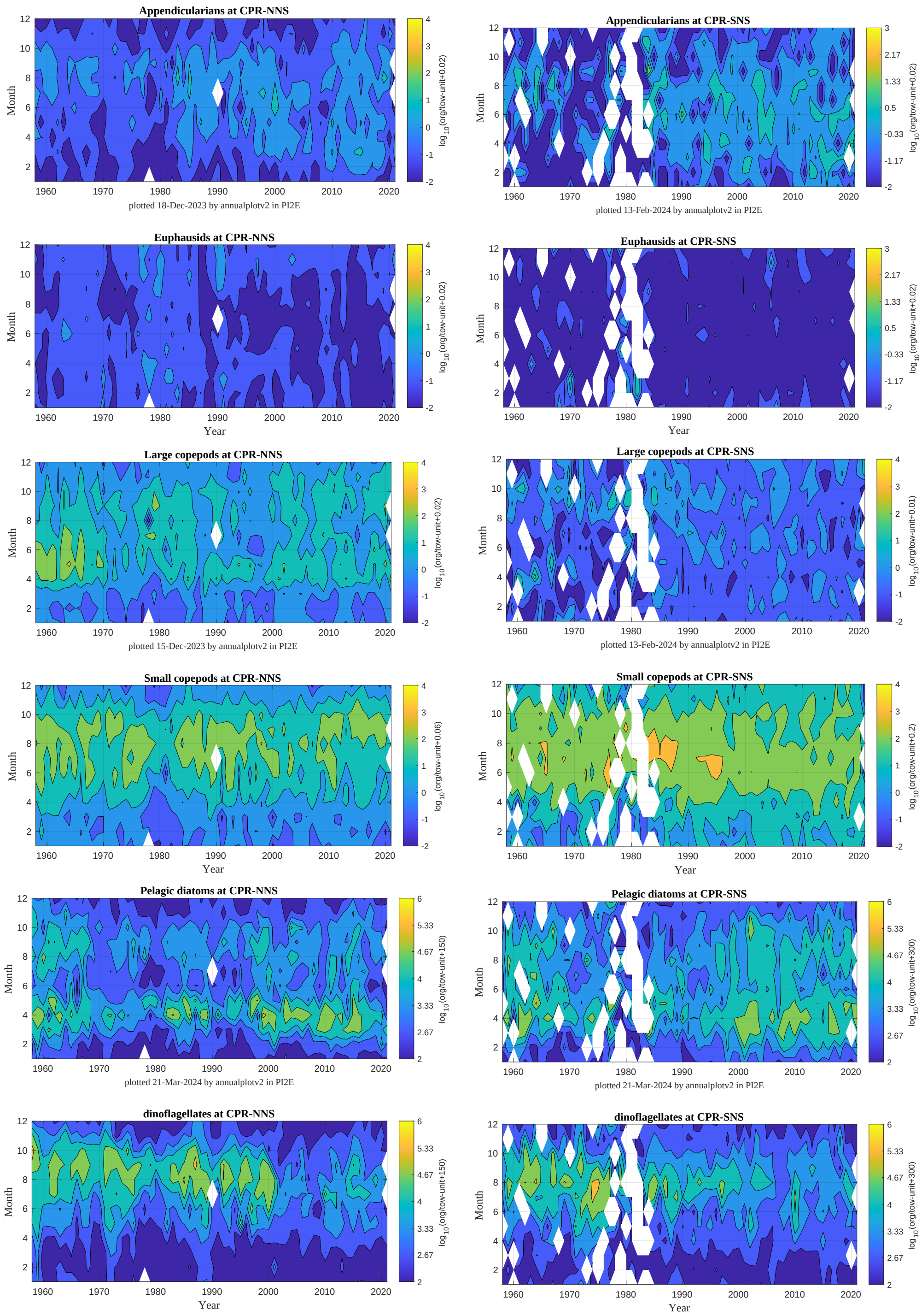

Figure 6: Lifeform contour plots for COMP4 areas: *left* Northern North Sea; *right* Southern North Sea. Both series commence in 1958, with some gaps in SNS during the early 1980s as a result of changes in CPR routes.

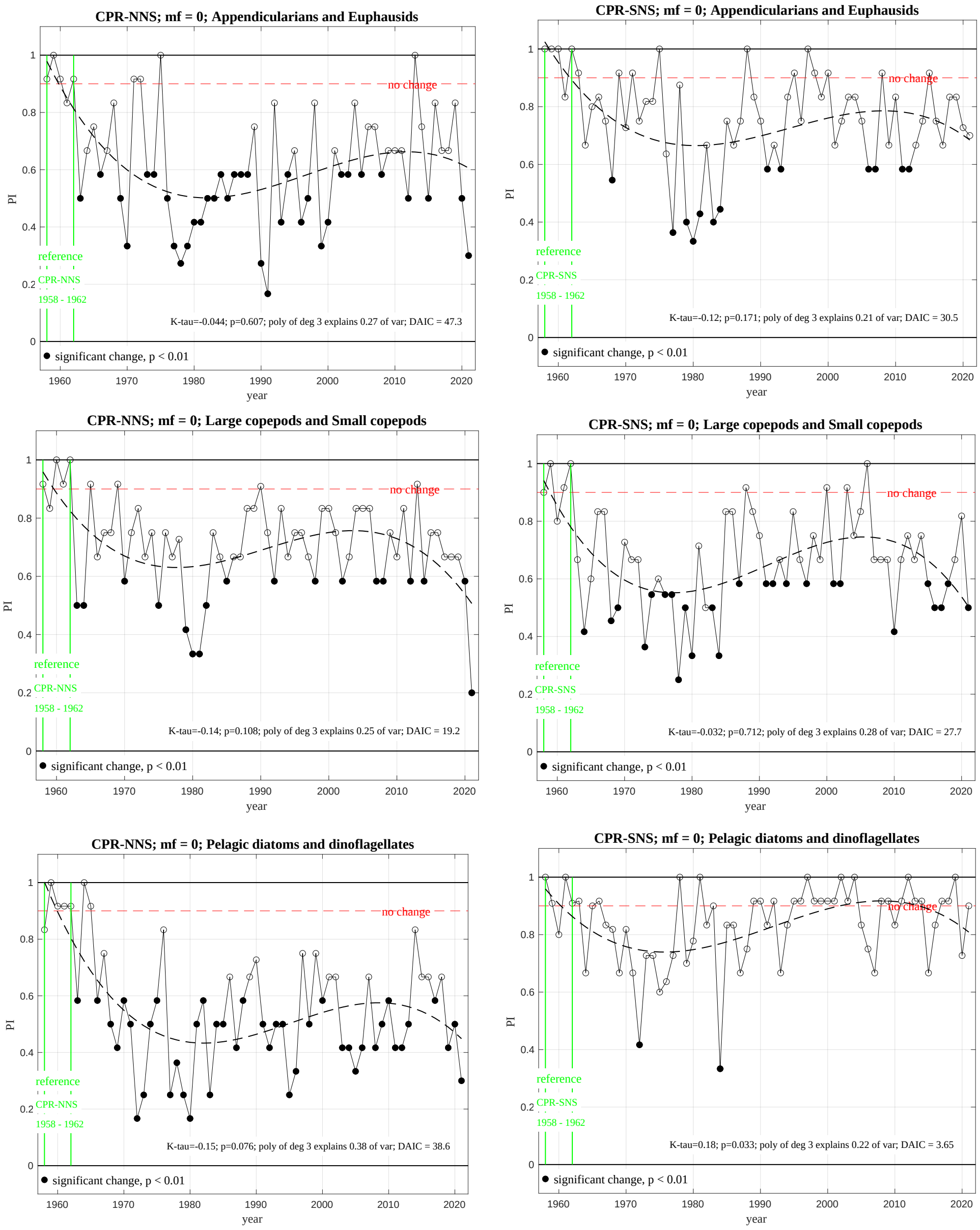

Figure 7: PI time-series plots for the COMP4 NNS (Northern Northern Sea, *left*) and SNS (Southern North Sea, *right*). In all examples shown here, a third-order polynomial explained a significant part of the variance in the annual values, whereas monotonic trends were weak.

5 Fish and fisheries

5.1 Fish stock

The concept of a *fish stock* is central to fisheries science but is not purely biological. **Stock** "defines semi-discrete groups of fish with some definable attributes of interest to [fishery] managers", the stock being "assumed homogenous for particular management purposes" (Begg et al., 1999). At different stages in its life, a single fish may use different food and environmental resources. For example, the main North Sea population of herring lays its eggs on gravel banks along the east coast of Britain; its young grow in shallow waters in the south-eastern North Sea, and the adults are found, and fished, mainly in the northern North Sea (ICES-HAWG, 2016; Engelhard et al., 2014). Sinclair and Iles (1989) raised the issue of how such migratory populations close their life-cycle, because the biological concept of stock is of a population of fish that maintains itself through breeding. *Spawning stock biomass* (SSB) is a measure of this aspect of stock; it is defined as the "total weight of all sexually mature fish in the stock" by ICES glossary. Fish are lost to the SSB through *natural and fisheries mortality*, and gained as young fish become mature and *recruit* to the breeding population. Less precisely defined is *Total Stock Biomass* (TSB), which includes the immature fish. An estimate of the TSB of plankton-eating fish would seem to provide a suitable indicator of PRESSURE (as a trophic boundary condition) on the plankton. SSB and TSB are routinely estimated from: information reported by fisheries (called *fisheries-dependent* (FD)); data obtained by fisheries research (called *fisheries-independent* (FI)); and mathematical models of stock dynamics that are constrained by FI and FD data.

Table 6: Planktivorous fish considered here; these are the main species of 'forage fish' caught by pelagic fisheries in the North Sea (NS) (Engelhard et al., 2014). (1) Trophic guild assignment and trophic level (TL) from supplemental material to Engelhard et al. (2011), which gives pout as a benthopiscivore. TL = 1 for phytoplankters, 2 for zooplankters feeding directly on phytoplankters, and 3 for planktivores feeding exclusively on zooplankters that have fed exclusively on phytoplankters. Information on prey plankton from Engelhard et al. (2014), ICES-Fishmap and Lindegren et al. (2018). See Table 3 for plankton lifeforms. (2) Trophic guild assignments from stomach content data for range of fish lengths (Thompson et al., 2022). (3) Relative importance of fishery to fish population dynamics. F is fisheries mortality and M is other mortality, for 1-year and older fish, 2001-2010 (Engelhard et al., 2014, table 3).

Fish	Life-cycle and distribution	(1) Guild, TL; prey	(2) Guild	(3) $\frac{F}{F+M}$
Family Clupeidae				
Herring, *Clupea harengus*	one main stock in NS: eggs laid on seabed near British coast; pelagic juveniles found in south-eastern NS; adults commonest in N NS	planktivore, TL 3.2; young: SCOP; adult: LCOP, EUPH, fish	planktivore at 3-67 cm	0.32
Sprat, *Sprattus sprattus*	one main stock in NS: pelagic eggs; pelagic adults commonest in S-E NS	planktivore, TL 3.0; young: DIA, SCOP; adults: APPEND, EUPH	planktivore at 6-21 cm	0.44
Family Gadidae				
Norway pout, *Trisopterus esmarkii*	one main stock in NS: pelagic eggs, pelagic adults commonest in N NS, where spend day near sea-bed	(?),TL 3.2; young: SCOP, APPEND; adults LCOP, EUPH	planktivore at 6-35 cm	0.08
Family Ammodytidae				
Sand-eel, *Ammodytes marinus*	several stocks: eggs laid in Winter in sand where adults live in burrows; water-column feeders, common in central NS	planktivore, TL 2.7; SCOP & LCOP	genus *Ammodytes*: planktivore at 7-27 cm	0.36
A. tobianus	summer spawning; included in fisheries statistics with *A. marinus*	planktivore, TL 3.2		

5.2 Planktivore fish

A *pelagic* fishery is one that takes place in the water-column, and the simplest definition of a pelagic fish is one that might be caught by this fishery. Whereas some pelagic fish (such as tuna) are predatory, the majority in seas around the UK have plankton as an important part of their diet. These pelagic *planktivores* typically form large shoals and are referred to as *forage fish* (Engelhard et al., 2014), because they provide the diet of larger fish, not to mention marine mammals and sea-birds. Table 6 lists the 4 species that make up most of the pelagic catch in the North Sea and which were the main subjects of this study.

Trophic guilds amongst fish are identified from feeding habits, and are thus somewhat analogous to lifeforms in the plankton. **Planktivores** are one these guilds. They feed primarily on invertebrate zooplankton but also on planktonic fish eggs and larvae and in some cases phytoplankton. *Planktopiscivores* prey on larger zooplankton and smaller fish.[3] These guild assignments are made on the basis of what is known about the diet of each sort of fish, which however changes as fish grow and with the availability of different sorts of prey in different seasons and different parts of the sea.

Over decades there have been major changes in pelagic fisheries, summarised by Engelhard et al. (2014) for the North Sea: different forage fish species have each dominated fisheries catches at different periods: from historical times until the 1950s, human consumption fisheries for herring; 1950s–1960s, industrial fisheries for young herring; 1970–1980s following herring collapse, industrial fisheries for Norway pout, sandeel, and sprat; 1990–2000s, industrial fishery predominated by sandeel and human consumption fishery for herring reinstated.

5.3 Fisheries Statistics

The FAO CWP online Handbook of Fishery Statistics lists several statistics related to what is taken by fisheries. Although the best statistic to use as an indicator of anthropogenic PRESSURE on pelagic systems would be *gross removal* - the total live weight of fish caught, or killed, during fishing operations, two others are more often available:

landings - the net weight of the fish products landed as officially recorded at the time of landing (after the catch has been processed or used at sea), and not including unrecorded (black market) landings);

[3] Other guilds include: *piscivores*, which as adults eat primarily fish and cephalopods; *benthopiscivores*, taking larger epifaunal invertebrates and fish; and *benthivores*, feeding mainly on epifaunal invertebrates (Engelhard et al., 2011).

catch - *retained catch* is the total live weight of fish retained during fishing operations; it excludes *discarded catch*, assumed to be non-viable when returned to the sea; in some cases an estimate of discards is added to retained catch.

For much of the history of fisheries, data for catch statistics came mainly from landings and was referred first to port of landing and then to internationally defined (large) sea-areas. ICES has worked to assess and improve the statistical reliability of these FD data (ICES, 2010; Lassen et al., 2012). In recent years, boats fishing in EU waters and larger than 12 m have been required to record catches in ship's logs, and even more recently these records have taken electronic form (Elliott and Holden, 2018, app. 4). The more recent data identify catch location more precisely.

5.4 Fish data for CPR areas, 1955 - 2011

The aim was obtain or construct time series of statistics for forage fish in the North Sea that were comparable with the time-series of PI values based on CPR data and starting in 1958. Methods are detailed in Appendix A. They involved drawing on several sources within ICES: the Stock Assessment Data Base (SAD), the Historic Catch Data Base (HCD), and Advice Publications. These included outputs from models as well as FI and FD data. Additional procedures were used to extend some of the time-series back towards 1958.

Before summing over the four forage fishes, the data for stock (SSB and TSB) and catch had to be assigned (Table 7) to the CPR areas in the North Sea that were used for the phytoplankton analysis. For herring, sprat and Norway pout, with only one main stock found in the North Sea, use was made of maps (Engelhard et al., 2014, Figure 1), which show the parts of the North Sea in which the main adult stock of each species, and the corresponding fishery, are located. The case of sandeels was more complex, because there are a number of distinct stocks in the North Sea.

Finally, the time-series of catch were summed to give series (Figure 8) for total (forage fish) **catch** in each CPR area of the North Sea, and the TSB series were summed to give TPB, **Total Planktivore Biomass**, in each area. In the case of the North area, TBP was calculated both with and without adult herring, on the grounds that the adults might be planktopiscivorous.

5.5 Fish data for COMP4 areas, 1997/2003 - 2016/2021

Whereas the earlier study used numerous assumptions in synthesising time-series for catch and TPB from model outputs as well as empirical (FD and

Table 7: Allocation of stocks and catches to CPR areas in the North Sea, based on Engelhard et al. (2014, figure 1). No sand-eel stock data available for North area, assumed zero catch. Pre-1982 sand-eel catch allocated to South area.

Area and CPR code	Herring	Herring juv	Sprat	Norway Pout	Sand-eel stocks
North - B1 + B2	1.0	0.2	0	1.0	SA5r + SA7r
Central - C1 + C2	0	0.5	0.2	0	SA3r + SA4
South - D1 + D2	0	0.3	0.8	0	SA1 + SA2r

FI) data, the later analyses used only empirical data that could be ascribed directly to COMP4 areas. This linked to the approach in PIT-PAF part A.

Two sets of data were used. The first contained all scientific Otter Trawl data for the four regions, taken from the ICES Database on Trawl Surveys (DATRAS: ICES, 2023) and Cefas's Fishing Survey System (FSS) database (Lynam and Ribeiro, 2022). Although these bottom trawls under-sampled forage fish (Walker et al., 2017; Nnanatu et al., 2020), it was assumed that undersampling was consistent and that the catch provided a reliable indicator of planktivore biomass change.

The Otter Trawl data-set was processed to provide annual time-series for each COMP4 region for the biomass (in kg km^{-2}) of the total of all fish identified as *planktivores* (Figure 9). These totals included more than the four forage fish listed in Table 6, and covered the years 1997 to 2021, although sampling in IRS had been sparse until 2008. There was very large variation in fish abundance (x) between individual Otter Trawl hauls; annual means were computed using a $log_{10}(x + z)$ transformation, where z was 0.7 times the minimum non-zero biomass of total planktivores.

The second data set contained Landings data assembled by the European Commission Scientific, Technical and Economic Committee for Fisheries (STECF) at stecf.jrc.ec.europa.eu/dd/fdi. It covered a shorter period (2003 - 2016) than the ICES SAD records described above, but specified catch location in ICES statistical rectangles (0.5° latitude by 1.0° longitude, or approx. 30×30 nautical miles). It was processed to extract and annually sum data for each forage fish in each of the four COMP4 areas (Figure 10). The landings time-series were then summed to give total forage fish **Landings**.

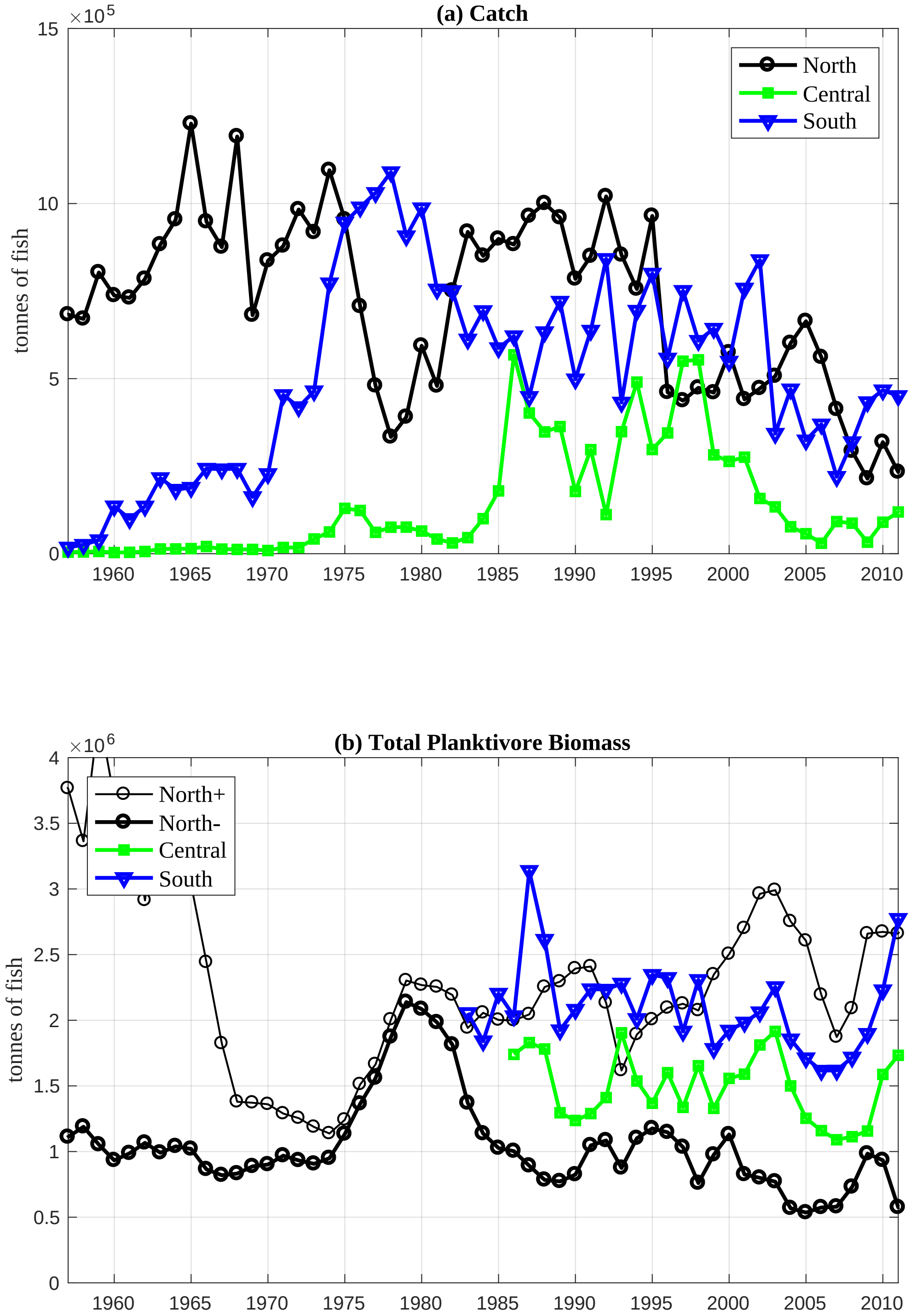

Figure 8: Synthesised time-series for the three traditional CPR areas of the North Sea. (a) **catch** Estimates of catch totalled over the four forage fishes. (b) **TPB**: estimates of stocks of planktivorous forage fish including juveniles. 'North+' includes adult herring, 'North-' excludes it.

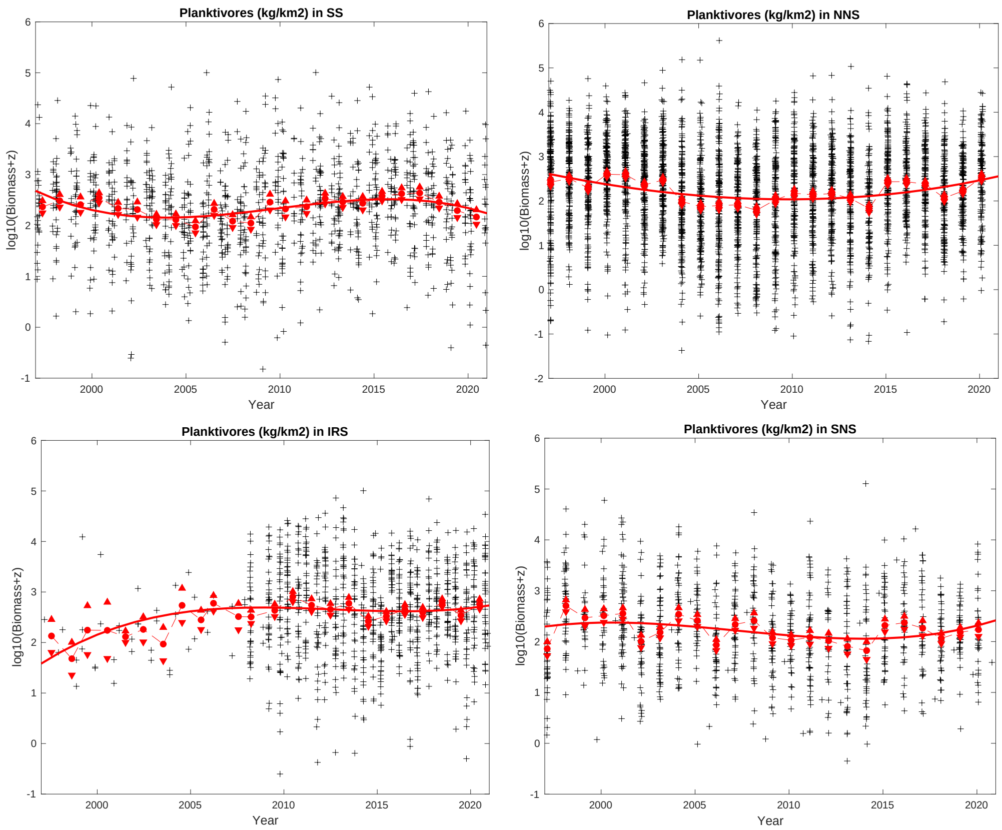

Figure 9: Research Otter Trawl planktivore time-series for COMP4 areas, processed from ICES DATRAS and Cefas FSS sources. The symbols + show (log) total planktivore biomass (kg km^{-2}) in each haul; red filled circles are annual ($\log_{10}(x+z)$) means $\pm$ 1 s.e. (red triangles), where z was 0.7 of the minimum non-zero sample value. The red line is fitted 3rd-order polynomial.

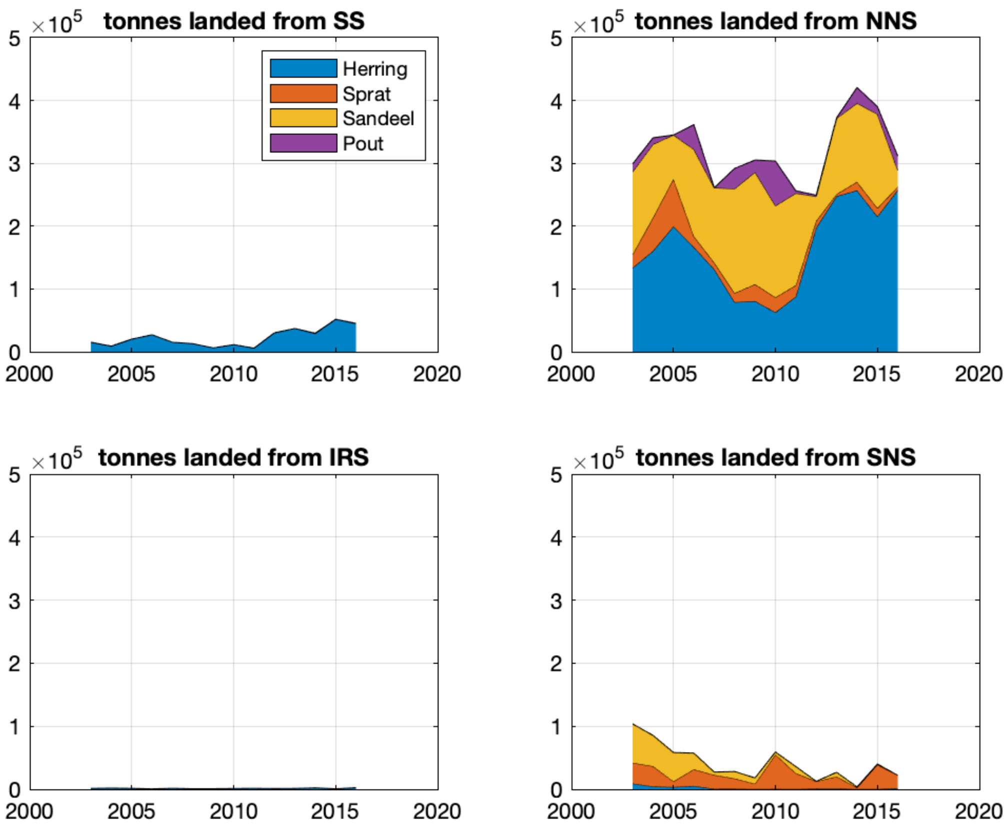

Figure 10: Forage Fish landings (tonnes wet weight, from STECF data) for COMP4 areas.

6 Correlation

6.1 Challenges

The aim of this study was to explore the relationships symbolised by $P \leftrightarrow S$ at the level of annual indicators of the time- and space- varying phenomena expressing the reality symbolised by $\mathbb{P}$ and $\mathbb{S}$. In contrast to the work in PIT-PAF part A, where thousands of values allowed fitting of multivariable models, the annual time-series considered here contained, at most, 63 values. Thus the focus was on simple, bivariate, relationships.

Nevertheless, even these were not without methodological challenges. One of these was from *autocorrelation*, a well-known problem in time-series correlations, because interpretation of statistical tests using least-squares depends on two assumptions. In the present case, the first is that time-series are *stationary*, meaning that the expected values and their variability do not change with time. The second is that each pair (P_i, S_i) is independent. The first assumption is falsified when there are long-term trends in the data, and the second where characteristics of the sampled populations (those symbolised as $\mathbb{P}$ and $\mathbb{S}$) persist from year to year. The standard solution is to difference the data (e.g. replace P_i, S_i by $\Delta P_i, \Delta S_i$), but this may prevent discovery of mutual trends (Pyper and Peterman, 1998), which is the main aim of the present work. However, seeking correlations between first-differenced time-series can be valuable when links are year-related: perhaps a year of especially high catch of forage fish has resulted in a particularly strong disturbance to the balance of organisms, shown by a PI value below the long-term trend. Sometimes such links are not immediate but show up in the following year or two, which can be investigated by testing for correlations where one time-series is lagged or advanced relative to the other.

6.2 Methods

Analyses were made with a Matlab script `CP2024` which called a number of standard and custom functions for correlation and regression. These included: correlations between lagged values and between difference values; using non-parameteric (Kendall, ranked) as well as parametric (Pearson, product-moment) correlation and regressions, as detailed in Table 8. Compensation for autocorrelation was made by reducing the degrees of freedom used to calculate significance (Pyper and Peterman, 1998).

Table 8: Summary of statistical tests used in the custom Matlab program `CP2024` and in some cases by the PI tool in `PI2E`. P and S are (annual values of) PRESSURE and STATE variables; T is time (in years). LFA = lifeform abundances; PI = Plankton Index (values). N is number of values (i.e. number of years) in a time-series, reduced to N^* where needed to compensate for autocorrelation. $\leftrightarrow$ refers to (symmetrical) correlation, $\mapsto$ refers to an (asymmetrical) mapping. In plots, p refers to probability of observing the result given a null hypothesis of no relationship, and p^* is the same but calculated from N^*.

relationship	statistic	explanation
$S(T)$	τ	Mann-Kendall test for monotonic trend in STATE (LFA, PI)
$T \leftrightarrow S$	ρ	Pearson correlation between STATE (LFA) and time
$T \mapsto S$	poly-1: r^2, b	linear regression of STATE (LFA) on Time, estimating trend rate b
$T \mapsto P$	poly-3: r^2, F	3rd order polynomial of PRESSURE on Time
$T \mapsto S$	poly-3: r^2, F	3rd order polynomial of STATE (PI) on Time
$P_T \leftrightarrow P_{T-h}$	$\rho(h)$	(Pearson) autocorrelation in a PRESSURE time-series with lags $h = 1 \ldots \frac{N}{4}$
$S_T \leftrightarrow S_{T-h}$	$\rho(h)$	(Pearson) autocorrelation in a STATE (PI) time-series with lags $h = 1 \ldots \frac{N}{4}$
$P \leftrightarrow S$	ρ, τ	Pearson and Kendall correlations between PRESSURE and STATE (PI)
$\Delta P \leftrightarrow \Delta S$	ρ, τ	Pearson and Kendall correlations between first differences of PRESSURE and STATE (PI)
$P \mapsto S$	poly-1: r^2, F	linear regression of STATE (PI) on PRESSURE as test for long-term association
$\Delta P \mapsto \Delta S$	poly-1: r^2, F	linear regression of first differences of STATE (PI) on those of PRESSURE as test for short-term association

6.3 Results

The strongest autocorrelations (exemplified in Figure 11) were found in the longest time-series (Table 13 in Appendix B.). However, compensation, by reducing degrees of freedom, was applied to all correlation analyses.

The following potential correlations were investigated:

- 6 pairs: total forage fish stock biomass (TPB), and forage fish catch, for the three CPR traditional areas and the diatom-dinoflagellate PI;

- 24 pairs: planktivore biomass, and forage fish Landings, for the four COMP4 areas and the three PI series PDIA-DINO, LCOP-SCOP, and APPEND-EUPH.

Only two significant correlations were found:

- between *Catch* and *diatom-dinoflagellate PI* for the CPR south area in the North Sea, 1958-2010 (figure 12)

- between *Landings* and *large-copepod-small-copepod PI* in the COMP4 Scottish Sea, 2003-2016 (figure 13).

Both these correlations were negative, meaning that increases in the fishery statistic corresponded to movement of the PI away from its reference condition. There were no correlations of first differenced or lagged time-series in either study.

Finally, the relationship between phytoplankton and zooplankton was analysed, treating the latter as PRESSURES on the former. There were 8 potential correlations: between LCOP-SCOP PI, or EUPH-APPEND PI, and PDIA-DINO PI, in each of the four COMP4 areas. Significant correlations were found:

- between EUPH-APPEND PI and PDIA-DINO PI in NNS;

- between LCOP-SCOP PI and PDIA-DINO PI in NNS;

- between LCOP-SCOP PI and PDIA-DINO PI in SNS.

All were positive, meaning that the pairs of lifeform pairs were behaving in similar fashion.

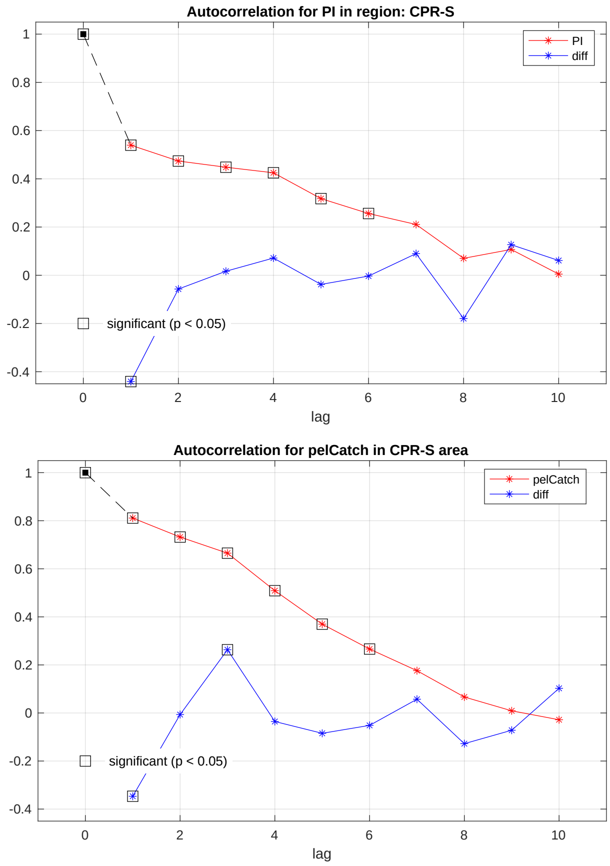

Figure 11: Autocorrelation in the time-series for *top*: the diatom-dinoflagellate PI, and *bottom*: the Catch of forage fisheries, for the CPR South area in the North Sea. These were amongst the strongest examples, with significant autocorrelation extending to lag 6, mostly eliminated, however, by first-differencing. $N = 53$, reduced to $N^* = 13$ after correction for the autocorrelation.

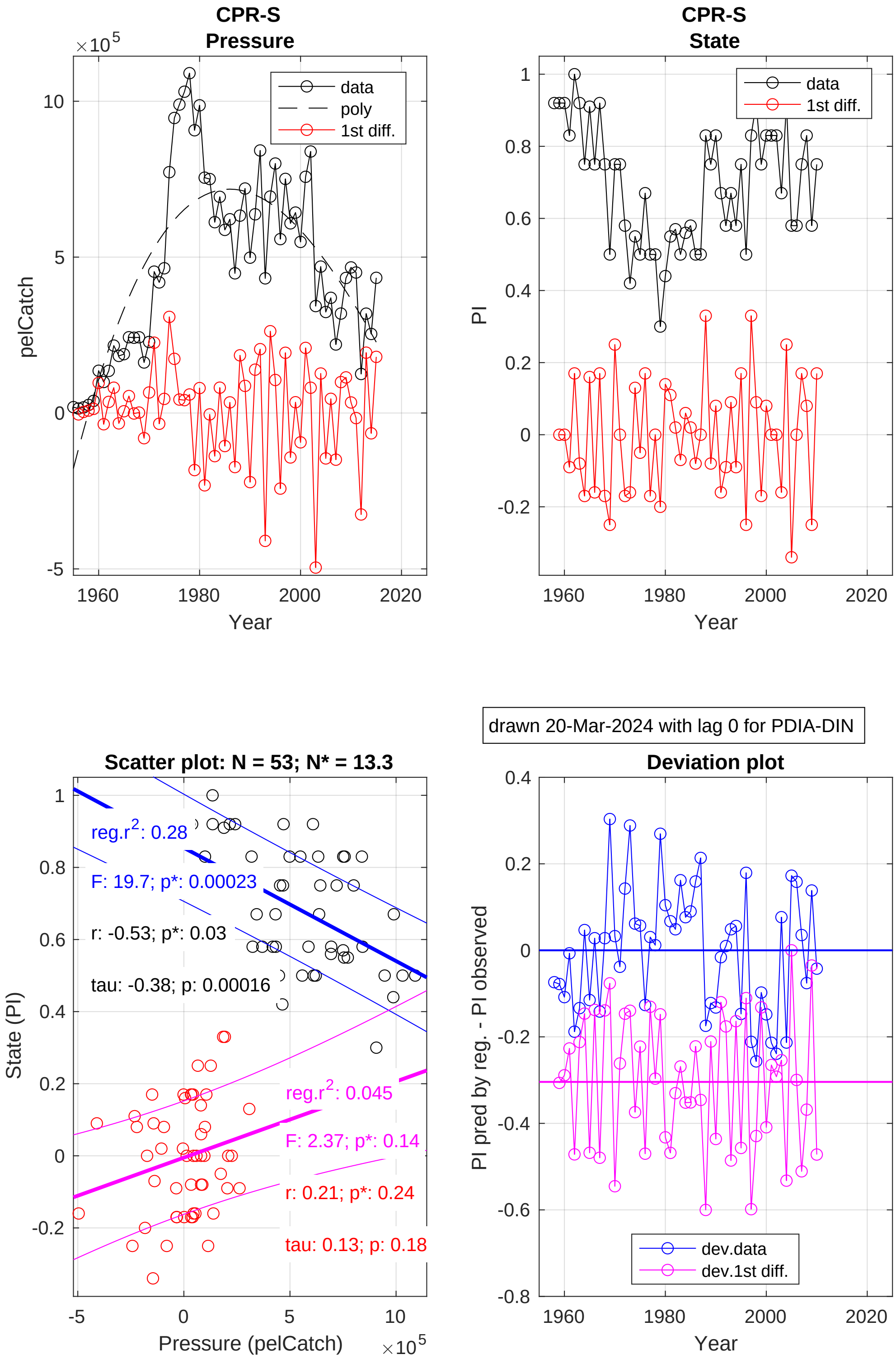

Figure 12: Significant correlation between the time-series for Catch from forage fisheries, and the PI time-series, for the CPR South area in the North Sea. *Left upper*: the Pressure series, a fitted third-order polynomial, and first derivative of the Pressure series. *Right upper*: the State series and its first derivative. *Lower left*: blue - regression of State on Pressure; red - regression of first differences. N^* and values of p^* for regression F-ratio and Pearson correlation r were corrected for autocorrelation. *tau* is the Kendall correlation. *Lower right*: deviations from the two regressions, those for differences offset.

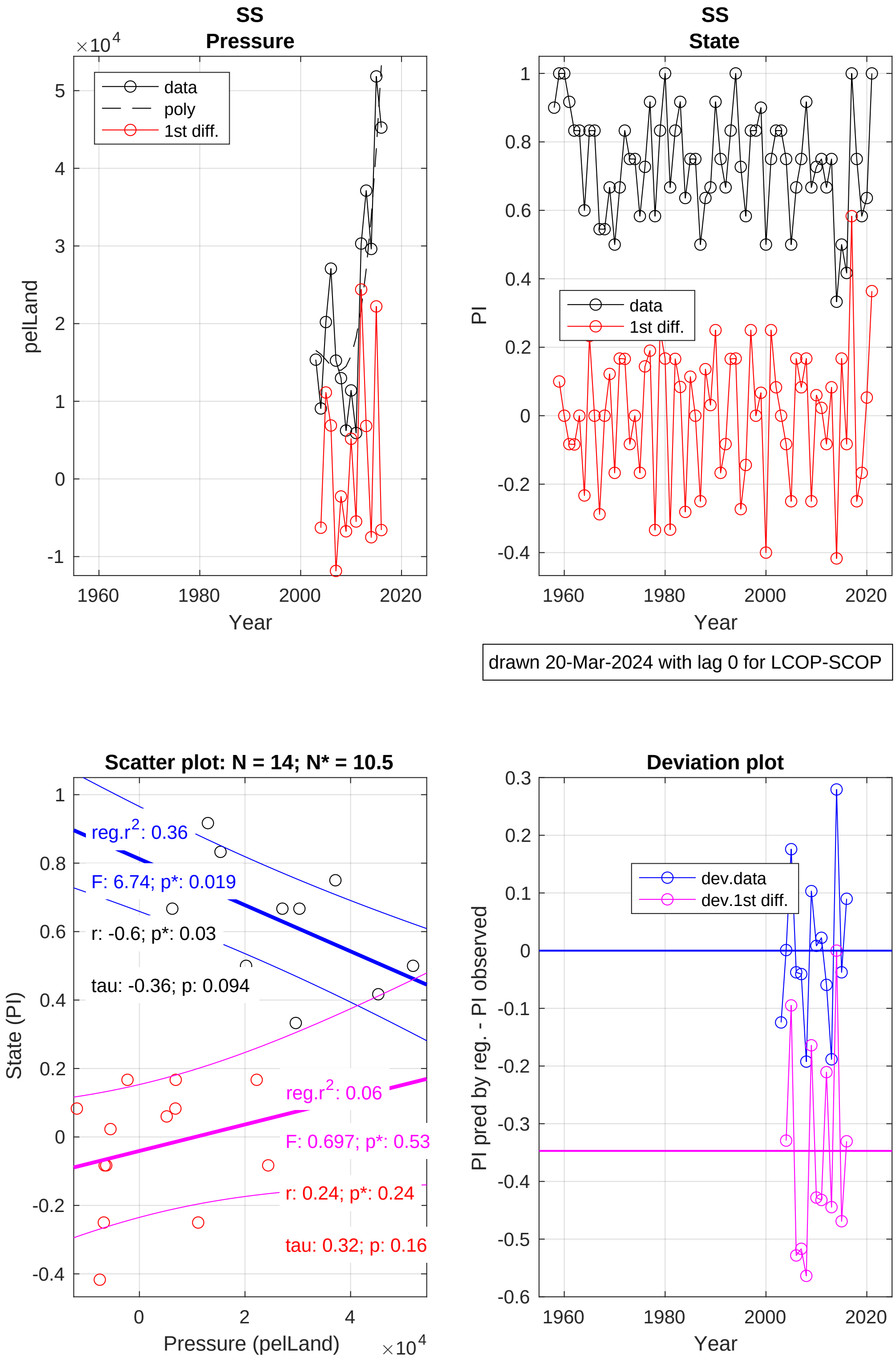

Figure 13: Significant correlation between annual Landings of forage fish (tonnes, from STECF data), and the PI series for the Large Copepod-Small Copepod lifeform pair, for the Scottish Sea. For further explanation, see text and Figure 12.

7 Discussion

This document has reported an analysis of correlations between plankton indicators, derived from Continuous Plankton Recorder (CPR) data, and data for stocks of, and catches from, planktivorous fish, in selected pelagic habitats around the UK. The analysis has focussed on annual statistics relating to (a) ICES statistical and 'traditional' CPR areas within the North Sea, and (b) selected examples of the COMP4 areas specified by OSPAR for the recent QSR. This spatiotemporal scale is larger than that at the focus of part A of PIT-PAF (Thompson et al., 2024), and the main interest of this part B has been in 'top-down' relationships, viewing stocks of planktivorous fish as trophic boundary conditions on pelagic habitats, and pelagic fisheries as anthropogenic pressures on pelagic systems.

The analysis of CPR data for the four COMP4 regions has shown significant changes in single lifeforms, and also significant trends in PI series for all three lifeform-pairs in both COMP4 areas within the North Sea (table 5). Other analyses of changes in plankton in the seas of N.-W. Europe (Bedford et al., 2020; Holland et al., 2023b) have reported trends in abundances in the PDIA, DINO, LCOP and SCOP lifeforms, and have linked them to climate change as shown by increasing sea-surface temperature. The present work adds findings about decreases in euphausiids (not hitherto considered as a lifeform by PHEG) and increases in appendicularians (part of the 'gelatinous' lifeform, which included ctenophora and cnidaria, but was found unsatisfactory by Holland et al. (2023b)).

These changes obviously have 'bottom-up' implications for planktivorous fish, especially where the fish select for different types of prey and where dietary requirements change as fish grow. However, the interest in this study has been in seeking correlations with pelagic fish and fisheries, and understanding the pelagic system in 'top-down' terms. Insofar as planktivore fish are the main consumers of some zooplanktonic lifeforms, it might be expected that changes in the fishes' abundance might impact directly on the balance amongst the zooplankters, and indirectly on the balance amongst the phytoplankters. Whereas there were several correlations between zooplankton and phytoplankton in the two COMP4 areas that are part of the North Sea, the links from fish and fisheries time-series to plankton lifeform pair PI time-series were weaker. This might have had several explanations:

- because the long time-series of catch and TPB for the 'traditional' CPR areas in the North Sea, were constructed using several assumptions that might not have been correct;
- because the research OtterTrawl time-series (at max. 24 years) and the

Fisheries Landings time-series (at max. 13 years for catches localised to ICES statistical rectangles) are as yet insufficiently long;

- because of a mismatch between scales relevant to fish biology and scales relevant to assessing pelagic habitats;
- because the complexities and feedback loops in pelagic food webs result in a resilient system that damps the effect of PRESSURE changes.

In part A of the PIT-PAF work, Thompson et al. (2024) recognised the difficulties in correlating changes in the abundances of zooplankters and forage fish, because of the different scales on which their dominant dynamics operated. They tackled this with two studies conducted at the *medium scale* of Table 1. The first used highly spatially resolved information that has been collected in a coordinated way across zooplankton and fish assemblages in the Celtic Sea and western English Channel. The second was a study across the northeast Atlantic that aimed to reveal larger scale spatial and temporal trends in fish body condition (fish weight at length) relevant to OSPAR biodiversity assessments. This work showed that, in general, at larger spatial scales, zooplankton abundance and the proportion of large copepods related positively with planktivorous fish body condition.

It is apparent that there is a spatiotemporal mismatch between the proper scales on which to assess fish stocks and the pelagic system, and those on which to assess plankton and the pelagic habitats. This mismatch is less in the case of fish such as sand-eels, with stocks localised within the North Sea, and greater in the case of fish such as herring, which circulate around most of the North Sea during their lifecycle. For maximum fish production, as the part A work has shown, the amount, type and quality of zooplankters in each feeding area must be optimal at the time when fish reach this area. So it would seem that resolving plankton-fish links on the scale of months in the Pelagic Habitat assessment areas (i.e. the COMP4 areas) may be key to making the links at the UK scale that are required for the valuation of the pelagic habitats' contribution towards provisioning ecosystem services.

8 Conclusions

There is clear evidence of change in the STATE of the pelagic habitats in the offshore waters assigned to the OSPAR COMP4 regions for the Irish Sea, Scottish Sea, Northern North Sea and Southern North Sea. However, although logic points to links between plankters and fish established through stomach content analyses, the analyses reported here for this *pelagic habitat* *assessment scale* have found only scant correlation between plankton indicators and fish/fisheries statistics. This may be because complex systems, such as the pelagic food web within shelf sea ecosystems, may not respond linearly to internally-generated or externally-forced change. Or because of the scale mismatch between, on the one hand, the assessment of fish stocks and pelagic fisheries, and on the other hand, the assessment of pelagic habitats. This conclusions apply equally to the ‘bottom-up’ perspective of fisheries science and the valuation of provisioning ecosystem services, and the ‘top-down’ perspective in which the pelagic fisheries are seen as amongst the PRESSURES on pelagic systems. In the latter case, it might be that fish influence the balance of organisms in the plankton less than do water temperatures or nutrient levels.

Finally, part A of the PIT-PAF study (Thompson et al., 2024) concluded that decreases in the abundance and size of plankton, as has been detected over large parts of the North Atlantic (Holland et al., 2023b; Pitois and Fox, 2006), and warming through climate change, represent deteriorating pelagic habitat conditions for planktivorous fish (Thompson et al., 2023). The changes in the abundances of planktonic lifeforms reported in this part B, especially those for euphausiids and appendicularians, add additional evidence concerning on-going change in pelagic habitats. As argued in more general terms by Dasgupta (2021), the crucial risk might be that of *regime shift* as ecosystems move beyond their *safe operating space*: i.e. a sudden change in pelagic habitats such that they no longer supply the ecosystem services on which the current pelagic fisheries depend. This risk reinforces the need (a) to continue to monitor the STATE of the pelagic habitats, and (b) to continue to regulate endogenous PRESSURES, including those from nutrients and excessive fishing, whilest contributing to international efforts to control global warming.

9 References

Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., Machairopoulou, M., Graves, C. A., Devlin, M., Milligan, A., Pitois, S., Mellor, A., Tett, P., and McQuatters-Gollop, A. (2020). Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. *Global Change Biology*, 26(6):3482–3497. DOI: 10.1111/gcb.15066.

Begg, G. A., Friedland, K. D., and Pearce, J. B. (1999). Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research*, 43(1-3):1–8.

Blauw, A., Eleveld, M., Prins, T., Zijl, F., Groenenboom, J., Winter, G., Kramer, L., Troost, T., Bartosova, A., Johansson, J., Capell, R., Eiola, K., Höglund, A., Tilstone, G., Land, P. E., Martinez-Vicente, V., Pardo, S., and van der Zande, D. (2019). Coherence in assessment framework of chlorophyll a and nutrients as part of the EU project 'Joint monitoring programme of the eutrophication of the North Sea with satellite data' (Ref: DG ENV/MSFD Second Cycle/2016). Activity 1 report, JMP EUNOSAT project. Available at: www.informatiehuismarien.nl.

Brito, A. C., Moita, T., Gameiro, C., Silva, T., Anselmo, T., and Brotas, V. (2015). Changes in the phytoplankton composition in a temperate estuarine system (1960 to 2010). *Estuaries and Coasts*, 38(5):1678–1691. DOI: 10.1007/s12237-014-9900-8.

Budria, A., Aubert, A., Rombouts, I., Ostle, C., Atkinson, A., Widdicombe, C., Goberville, E., Artigas, F., Johns, D., Padegimas, B., Corcoran, E., and McQuatters-Gollop, A. (2017). Cross-linking plankton indicators to better define GES of pelagic habitats. Deliverable WP1.4, EcApRHA project (Applying an Ecosystem Approach to (sub) Regional Habitat Assessment). Available at: www.ospar.org/work-areas/bdc/ecaprha/reports.

Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S. M., and Engelhard, G. H. (2018). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24(1):e352–e364.

Cochrane, S., Connor, D., Nilsson, P., Mitchell, I., Reker, J., Franco, J., Valavanis, V., Moncheva, S., Ekebom, J., Nygaard, K., Santos, R. S., Naberhaus, I., Packeiser, T., van de Bund, W., and Cardoso, A. (2010). Marine Strategy Framework Directive: Task Group 1 Report: Biological diversity. Technical report, European Commission JRC-Ispra and ICES, Luxembourg: Office for Official Publications of the European Communities.

Dasgupta, P. (2021). The Economics of Biodiversity: The Dasgupta Review. Technical report, HM Treasury, London. Available from: assets.publishing.service.gov.uk.

Elliott, M. and Holden, J., editors (2018). *UK Sea Fisheries Statistics 2017*. Marine Management Organisation, London.

Engelhard, G. H., Ellis, J. R., Payne, M. R., ter Hofstede, R., and Pinnegar, J. K. (2011). Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES Journal of Marine Science*, 68(3):580–591. DOI: 10.1093/icesjms/fsq183.

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A., Scott, F., Brunel, T., Aarts, G., Kooten, T. v., and Dickey-Collas, M. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science*, 71(1):90–104. DOI: 10.1093/icesjms/fst087.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., and Wanless, S. (2006). From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, 75(6):1259–1268.

Gowen, R., Collos, Y., Tett, P., Scherer, C., Bec, B., Abadie, E., Allen, M., and O'Brien, T. (2015). The response of diatom and dinoflagellate lifeforms to reduced phosphorus loading: a case study in the Thau Lagoon. *Estuarine, Coastal and Shelf Science*, 162:45–52. DOI: 10.1016/j.ecss.2015.03.033.

Graves, C., Best, M., Atkinson, A., Bear, B., Bresnan, E., Holland, M., Johns, D., Machairopoulou, M., McQuatters-Gollop, A., Mellor, A., Ostle, C., Paxman, K., Pitois, S., Tett, P., and Devlin, M. (2023). At what scale should we assess the health of pelagic habitats? trade-offs between small-scale manageable pressures and the need for regional upscaling. *Ecological Indicators*, 154(art. no. 110571):15. DOI: 10.1016/j.ecolind.2023.110571.

Hardy, A. C. (1924). The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. *Fishery Investigations, Series II*, 7(3):1–53.

Heath, M. R. (2005a). Changes in the structure and function of the North Sea fish foodweb, 1973-2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*, 62(5):847–868.

Heath, M. R. (2005b). Regional variability in the trophic requirements of shelf sea fisheries in the Northeast Atlantic, 1973-2000. *ICES Journal of Marine Science*, 62(7):1233–1244.

Heath, M. R. and Beare, D. J. (2008). New primary production in northwest European shelf seas, 1960-2003. *Marine Ecology-Progress Series*, 363:183–203.

Holland, M., Louchart, A., Artigas, L. F., and McQuatters-Gollop, A. (2023a). Changes in phytoplankton and zooplankton communities. In *The 2023 Quality Status Report for the Northeast Atlantic*. OSPAR Commission, London. URL: oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023.

Holland, M. M., Louchart, A., Artigas, L. F., Ostle, C., Atkinson, A., Rombouts, I., Graves, C., Heyden, B., Machairopoulou, M., Bresnan, E., Schilder, J., Jakobsen, H., Lloyd-Hartley, H., Tett, P., Best, M., Goberville, E., and McQuatters-Gollop, A. (2023b). Major declines in NE Atlantic plankton contrast with more stable populations in the rapidly warming North Sea. *Science of the Total Environment*, 898:no. 165505, 14 pp.

Huse, G., Salthaug, A., and Skogen, M. D. (2008). Indications of a negative impact of herring on recruitment of Norway pout. *ICES Journal of Marine Science*, 65(6):906–911.

ICES (2010). Report of the Workshop on methods to evaluate and estimate the precision of fisheries data used for assessment (WKPRECISE), 8-11 September 2009, Copenhagen, Denmark. ICES CM 2009/ACOM 40, ICES, Copenhagen.

ICES (2023). Database on trawl surveys (datras). Technical report, ICES, Copenhagen, Denmark. datras.ices.dk.

ICES-HAWG (2016). Herring (*Clupea harengus*) in subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak and Kattegat, eastern English Channel). Stock Annex her-47d3_SA, ICES Herring Assessment Working Group for the Area south of 62 °N (HAWG), Copenhagen. URL ices.dk/sites/pub/Publication Reports/Stock Annexes/2016/her-47d3_SA.pdf.

Lassen, H., Cross, D., and Christiansen, E. (2012). One Hundred Years of Catch Statistics for the Northeast Atlantic. Cooperative Research Report 311, ICES, Copenhagen.

Lindegren, M., Van Deurs, M., MacKenzie, B. R., Worsoe Clausen, L., Christensen, A., and Rindorf, A. (2018). Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study. *Fisheries Oceanography*, 27(3):212–221.

Luiten, H. (1999). A legislative view on science and predictive models. *Environmental Pollution*, 100(1-3):5–11.

Lynam, C. and Ribeiro, J. (2022). A data product derived from Northeast Atlantic groundfish data from scientific trawl surveys 1983-2020. Cefas datahub. DOI: 10.14466/CefasDataHub.126.

Mak, Y. L., Tett, P., Yung, Y. K., Sun, W. C., Tsang, H. L., Chan, C. T., Liu, H., Chiu, W. L., Leung, K. F., Yang, R., and Chui, H. K. (2024). Phytoplankton Community Integrity Index (PCII) – A potential supplementary tool for evaluating nutrient enrichment status of Hong Kong marine waters. *Marine Pollution Bulletin*, 199(art. no. 115964):16. DOI: 10.1016/j.marpolbul.2023.115964.

Margalef, R. (1978). Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta 1*, 1:493–509.

McQuatters-Gollop, A., Atkinson, A., Aubert, A., Bedford, J., Best, M., Bresnan, E., Cook, K., Devlin, M., Gowen, R., Johns, D. G., Ostle, C., Scherer, C., and Tett, P. (2019). Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy. *Ecological Indicators*, 101:913–925. DOI: 10.1016/j.ecolind.2019.02.010.

Nnanatu, C. C., Thompson, M. S. A., Spence, M. A., Couce, E., van der Kooij, J., and Lynam, C. P. (2020). Bayesian hierarchical space-time models to improve multispecies assessment by combining observations from disparate fish surveys. arXiv. arxiv.org/abs/2012.02196.

ONS (2017). Principles of Natural Capital Accounting. Background paper, Office for National Statistics, London. ONS: principles of natural capital accounting.

ONS (2023). Principles of UK natural capital accounting: 2023. Methodology, Office for National Statistics, London. URL: www.ons.gov.uk - Principles of Natural Capital Accounting.

Pitois, S. G. and Fox, C. J. (2006). Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. *ICES Journal of Marine Science*, 63(5):785–798. DOI: 10.1016/j.icesjms.2006.03.009.

Pyper, B. J. and Peterman, R. M. (1998). Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(9):2127–2140. DOI: 10.1139/f98-104.

Reid, P., Lancelot, C., Gieskes, W., Hagmeier, E., and Weichart, G. (1990). Phytoplankton of the north sea and its dynamics - a review. *Netherlands Journal of Sea Research*, 26:295–331.

Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D., and Witte, M. (2006). Using continuous plankton recorder data. *Progress in Oceanography*, 68(1):27–74. DOI: 10.1016/j.pocean.2005.09.011.

Rodhe, J., Tett, P., and Wulff, F. (2006). Chapter 26. the Baltic and North seas: a regional review of some important physical-chemical-biological interaction processes. In Robinson, A. R. and Brink, K. H., editors, *The Sea, Volume 14B, The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses: The Coasts of Africa, Europe, Middle East, Oceania and Polar Regions*, pages 1033–1075. Harvard University Press, Cambridge, Mass.

Rombouts, I., Simon, N., Aubert, A., Cariou, T., Feunteun, E., Guérin, L., Hoebeke, M., McQuatters-Gollop, A., Rigaut-Jalabert, F., and Artigas, L. (2019). Changes in marine phytoplankton diversity: Assessment under the Marine Strategy Framework Directive. *Ecological Indicators*, 102:265 – 277. DOI: 10.1016/j.ecolind.2019.02.009.

Sinclair, M. and Iles, T. D. (1989). Population regulation and speciation in the oceans. *Journal du Conseil permanent international pour l'Exploration de la Mer*, 45(2):165–175.

Tett, P. (2016). Artefacts and the PI: Supplemental Material 2 for the manuscript: Relating changes in pelagic ecosystem state shown by the Plankton Index to changes in exogenous and endogenous pressures, using CPR data from the North Sea (Gowen et al.). Unpublished report, SAMS, Oban, Scotland.

Tett, P., Best, M., Faith, M., and Bresnan, E. (2024). Natural capital in plankton: theory development for valuing a dynamic system with rapid turnover which typifies marine plankton: v.2. Report to UK Department for Environment, Food and Rural Affairs, by UK Pelagic Habitats Expert Group, SAMS, Oban, Scotland.

Tett, P. and Bresnan, E. (2018). Assessment of CPR data: Supplemental Material 1 for the manuscript: Relating changes in pelagic ecosystem state shown by the Plankton Index to changes in exogenous and endogenous pressures, using CPR data from the North Sea (Gowen et al.). Unpublished report, SAMS, Oban, Scotland.

Tett, P., Carreira, C., Mills, D., van Leeuwen, S., Foden, J., Bresnan, E., and Gowen, R. (2008). Use of a Phytoplankton Community Index to assess the health of coastal waters. *ICES Journal of Marine Science*, 65:1475–1482. DOI: 10.1093/icesjms/fsn161.

Tett, P., Gowen, R., Mills, D., Fernandes, T., Gilpin, L., Huxham, M., Kennington, K., Read, P., Service, M., Wilkinson, M., and Malcolm, S. (2007). Defining and detecting Undesirable Disturbance in the context of Eutrophication. *Marine Pollution Bulletin*, 53:282–297. DOI: 10.1016/j.marpolbul.2006.08.028.

Thompson, M., Lynam, C., and Preciado, I. (2022). Pilot assessment of feeding guilds. In *OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic*, number 856/2022. OSPAR COMMISSION, London. Available at: oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023.

Thompson, M. S., Greig, L., Scott, J., Griffin, K., and Tett, P. (2024). Establishing good pelagic habitat conditions for planktivorous fish. Cefas report for Putting it together: Plankton and Fisheries (PIT PAF). Cefas manuscript and report.

Thompson, M. S. A., Couce, E., Schratzberger, M., and Lynam, C. P. (2023). Climate change affects the distribution of diversity across marine food webs. *Global Change Biology*, 29(23):6606–6619. 10.1111/gcb.16881.

Turner, R. K., Schaafsma, M., Mee, L., Elliott, M., Burdon, D., Atkins, J. P., and Jickells, T. (2015). Conceptual framework. In Turner, R. K. and Schaafsma, M., editors, *Coastal zones ecosystem services: From science to values and decision making*, Studies in Ecological Economics, chapter 2, pages 11–40. Springer.

UN (2021). System of Environmental-Economic Accounting— Ecosystem Accounting (SEEA EA). White cover publication, pre-edited text subject to official editing, United Nations. Available at: seea.un.org/ecosystem-accounting.

van Leeuwen, S. M., Tett, P., Mills, D. K., and van der Molen, J. (2015). Stratified areas in the North Sea: long-term variability and biological and policy implications. *Journal of Geophysical Research: Oceans*, 120:4670–4686. DOI: 10.1002/2014JC010485.

Walker, N. D., Maxwell, D. L., Le Quesne, W. J. F., and Jennings, S. (2017). Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, 74(5):1448–1457. DOI: 10.1093/icesjms/fsw250.

Wyatt, T. (2014). Margalef's mandala and phytoplankton bloom strategies. *Deep-Sea Research II*, 101:32–49. DOI: 10.1016/j.dsr2.2012.12.006.

Appendices

A Methods for synthesised fish time-series, 1958-2010

This appendix gives details, in tabular form, of the sources of data and the methods used with the fisheries statistics for 1958 - 2010, which allowed the construction of the synthesised fish/fisheries time-series in figure 8. Tables 9, 11 and 10 list the ICES data sources, and Table 12 describes the assembly of biomass and catch time-series for each fish.

Table 9: ICES Stock Assessment Database (SAD) contains documents with assessments of particular **stocks** and includes annual values for *SSB*, *Catch* and in some cases *Landings* as well as other statistics. SSB and Catch data presented in tonnes, although there may have been an error in the case of SA1. ICES IV is North Sea, IIIa is Skagerak-Kattegat.

species	file (of type `.doc`)	comment
Herring: N. Sea autumn spawners (IV, IIIa, VIId)	`7689_her-47d3_2016_7689_201715143402`	
Sprat: N. Sea (IV)	`7181_spr-nsea_2016_7181_201715143402`	landings, not catch
Norway pout (IV, IIIa), autumn assessment	`7998_nop-34-oct_2016_7998_201715143402`	
sand-eel SA1	`8229_san.sa.1r_2017_8229_201732104452`	catch data interpreted as kg
sand-eel SA2	`8231_san.sa.2r_2017_8231_201732104739`	
sand-eel SA3	`8235_san.sa.3r_2017_8235_201732105732`	
sand-eel SA4	`8230_san.sa.4_2017_8230_201732110820`	
sand-eel SA5	`8199_san.sa.5r_2017_8199_201732111827`	catch only
sand-eel SA7	`8201_san.sa.7r_2017_8201_201732112808`	catch only

Credit: ICES Stock Assessment Database. Copenhagen, Denmark. ICES. http://standardgraphs.ices.dk, [accessed March 2017].

Table 10: ICES Advice publications, and related data, up to 2016, had been assembled by Cefas in a spreadsheet `Forage Fish Stock data.xlsx` (FFSD). → below means: follow hyperlink.

Herring in Subarea IV and Divisions IIIa and VIId (North Sea autumn spawners): **TSB**	standardgraphs.ices.dk/stockList → assessment year 2016, FishStock her47-d3. → 'View source data' → column `TBiomass`; central estimates used; series commences 1947.
Sprat in Subarea IV (North Sea) : **TSB**	standardgraphs.ices.dk/stockList → assessment year 2016, FishStock spr-nsea → 'View source data' → column `TBiomass`; central estimates used; series commences 1974.
Norway Pout in Subarea IV (North Sea) and IIIa (Skagerrak - Kattegat) - Autumn assessment: **TSB**	standardgraphs.ices.dk/stockList → assessment year 2016, FishStock nop-34-oct → 'View source data' → column `TBiomass`; central estimates used; series commences 1984.
Sandeel in Dogger Bank area (SA1). Area roughly approximates D2.	Advice/2016/2016/san-ns1.pdf No TSB data; SSB used: may include 0-group fish (unclear); starts 1983
Sandeel in Central and South North Sea (SA2). Area roughly approximates D1.	Advice/2016/2016/san-ns2.pdf No TSB data; SSB used: may include 0-group fish (unclear); starts 1983
Sandeel in Skagerrak and Kattegat, North and Central North Sea (SA3). Area roughly approximates C1.	Advice/2016/2016/san-ns3.pdf No TSB data; SSB used: may include 0-group fish (unclear); starts 1983
Sandeel in North and Central North Sea (SA4). Area roughly approximates C2.	Advice/2016/2016/san-ns4.pdf No stock data.
Sandeel in Northern North Sea, Viking and Bergen banks (SA5). Area roughly approximates B1.	Advice/2016/2016/san-ns5.pdf No stock data.
Sandeel in Northern North Sea, Shetland (SA7). Area roughly approximates B2.	Advice/2016/2016/san-ns7.pdf No stock data.

In summary, the sources were: standardgraphs.ices.dk/stockList and www.ices.dk/sites/pub/Publication Reports/Advice/

Table 11: ICES Historic Catch Data Base.

A single Excel spreadsheet that can be analysed as a database, providing **Catch** data (only) for 1950 – 2010, which were used to extend time-series.

ICES did not provide a form of citation when accessed in March 2017. The source was 'ICES Historical Nominal Catches 1950-2010' available from www.ices.dk/marine-data/Documents/CatchStats/HistoricalLandings1950-2010.zip

Table 12: Details of procedures for calculating Total Catch and TPB; see also table 7 for allocations of stock to areas.

	Total **Catch**
herring	all data from SAD catch
sprat	SAD landings data after 1973-8, before that HCD
Norway pout	SAD catch data after 1983-88, before that HCD
sand-eels	SAD catch data after 1982-86 (depending on region), before that N and C assumed 0 and all HCD sand-eel allocated to South
	Total Planktivore Biomass **TPB**
herring	juveniles estimated from FFSD TSB minus SAD SSD
sprat	smoothed FFSD TSB (from 1974)
Norway pout	FFSD TSB from 1984; before this, TSB estimated from SSB (B) using $TSB = 1.552E^{-10}B^3 - 7.973E^{-05}B^2 + 14.02B - 228000$ (calculated from post-1984 SAD SSB and FFSD TSB), where pre-1984 SSB was itself estimated (Huse et al., 2008) from FFSD herring TSB
sand-eels	variously labelled SSB or TSB in FFSD (from 1983)

B Autocorrelation

Table 13: Autocorrelation analyses of time-series. AC refers to autocorrelation, with significance at each lag estimated from Pearson ρ and $p < 0.05$ with cut-off at $\frac{N}{4}$. A minus lag indicates a negative correlation. 'ns' refers to no significant correlation at any lag up to $\frac{N}{4}$, and the $rho = 1$ correlation at lag 0 has been ignored. N gives the number of years used in the analysis, set by the shortest of the two time-series used in each correlation calculation.

Area	Time-series	Years available	N used	AC sig	AC sig first diff.
Traditional CPR areas					
North	PI	1958-2010	53	to lag 4	at lag 1,6
Central	PI	1958-2010	53	to lag 3	at lag 1
South	PI	1958-2010	53	to lag 6	at lag 1
North	FF catch	1957-2011	53	to lag 3	ns
Central	FF Catch	1957-2011	53	to lag 8	at lag 6
South	FF Catch	1957-2011	53	to lag 6	at lag 1,3
North	TPB	1957-2011	53	to lag 5 at lag -9,-10	ns
Central	TPB	1986-2011	26	to lag 4	at lag 1
South	TPB	1983-2011	29	at lag 1,-4	ns
COMP4 areas					
IRS	PI COP	1970-2021	12	ns	ns
SS	PI COP	1958-2021	24	ns	at lag -1
NNS	PI COP	1958-2021	24	at lag -3	at lag -1
SNS	PI COP	1958-2021	24	at lag -4	to lag (+/-)4 at lag 6
IRS	FF Landings	2003-2016	14	ns	ns
SS	FF Landings	2003-2016	14	to lag 1	ns
NNS	FF Landings	2003-2016	14	ns	ns
SNS	FF Landings	2003-2016	14	ns	ns
IRS	TPB	2008-2021	12	ns	ns
SS	TPB	1997-2021	24	to lag 2	ns
NNS	TPB	1997-2020	24	to lag 1	ns
SNS	TPB	1997-2020	24	ns	ns