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Report of the ICES/GLOBEC Working Group on Life Cycle and Ecology of Small Pelagic Fish (WGLESP)

By Correspondence

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Executive summary

WGLESP worked by correspondence in 2008 to compile knowledge, allowing for setting new perspectives. A CRR is being finalized, which documents life cycle patterns, their relationship with oceanographic features and the potential impacts of climate on them. The document is expected to be ready before the end of 2008.

Past activities of the group, related workshops and theme sessions were reviewed. Pelagic fish population responses to external environmental forcing were understood to be modulated by behaviour and thus populations' substructure. Means of how to model habitat characteristics and predict fish distributions using outputs of lower trophic ecosystem models have been suggested. Impacts of regime shifts in the lower trophic levels on pelagic fish occurrence have been demonstrated. The activity of the group so far can be summarized under three topics:

- Identification of patterns and changes in these;
- Modelling habitat occupation;
- Understanding how external forcing interacts with biological factors (population substructure and interspecific interactions).

A future perspective is to work within the frame work of climate change and ecosystem effects on pelagic fish populations, in relation with SGCC. For that, links with a group on operational oceanographic products, WGZE for zooplankton production, WGPBI for modelling, WGSAEM for change detection in patterns, and SIMWG for population substructure, are seen as potentially useful.

1 ToR a) Prepare a document compiling the knowledge assembled by SGRESP on life cycle patterns and mesoscale oceanographic features for small pelagic fish in the North East Atlantic, to be proposed for publication as a Cooperative Research Report

The CRR project is intended to document life cycle patterns and how they match physical features, for small pelagic fish stocks in the North East Atlantic (ICES waters). The material has been selected from past reports and the contents of the document have been agreed. The document to be submitted for publication as a CRR will have the following contents: Introduction, One section for each population (ID card), Conclusion.

The list of populations is: NEA mackerel, NEA blue whiting, herring (Norwegian spring-spawning, North Sea, Celtic Sea, NW of Ireland), sprat (Baltic Sea, North Sea), SWE sardine, Biscay anchovy. Population ID cards will follow the same template, which will have the following sections: Life History Traits, Wintering, Spawning, Feeding, Migrations, Larval Drift and nursery areas, Long term trends, Present characteristics, Potential environmental influence. In addition, a conceptual diagram of the life cycle pattern will illustrate the ID card as well as a diagram of the oceanographic features that potentially affect the habitats and life cycle pattern. The conclusion will discuss schematics for life cycles, importance of behaviour, perspectives on modelling and use of operational oceanographic products. ID cards are being updated. The document is expected to be finalized for the attention of LRC before the end of 2008.

2 ToR b) Summarise outcomes from past activity (e.g. SGRESP, OSPAR request, 2006 Theme Session B, 2007 Theme Session G, WKLTVSWE, WKTEST) to document the mechanisms and controls of changes in spatial distributions and migration patterns

The life cycles of fish populations are organized geographically. Recent work within ICES has revisited the topic of the controls of fish spatial distributions and migration patterns for predicting climate change effects as well as for the conservation of essential habitats. The work is here summarized. Controls on fish spatial distributions and migration patterns are both external and internal to the populations. External factors are driven by environmental forcing and will affect habitat suitability as well as migration cues. Internal factors relate to stock abundance, density-dependence, age structure, fish condition, contingent diversity and behaviour including learning. Internal factors will modulate populations' response to hydro-climate forcing or the way populations recover after collapse. Fishing will impact the interaction between a population and its environment, as it will modify population abundance, demography and contingent diversity.

Patterns and concepts

SGRESP (2004–2006) documented the spatial patterns of the life cycles of different populations of pelagic species in ICES waters (herring, mackerel, sardine, sprat and anchovy) as well as the match of these patterns with regional and seasonal oceanographic features. The idea of a match between life cycle geographic organization and oceanographic structures built on the concepts developed by Sinclair (1988) and Bakun (1996). Hydro-climatic forcing on the drift and retention of larval stages is commonly identified as critical for life cycle closure. But the importance of adult fish spatial behaviour in selecting spawning grounds was the key in determining the interaction between the climate conditions and the fish populations. Changes in spawning windows in space and time were identified for sprat and anchovy, as well as spawning migration and nursery grounds for mackerel. Changes in spawning and wintering grounds were reported for herring that were determined by behaviour and fish condition. A shift in the extension of spawning areas for Atlanto-Iberian sardine, unrelated to the population biomass has also been reported. Environmental forcing alone cannot be expected to explain changes in distribution, unless changes are so strong that they over-ride all other drivers. Internal factors (e.g. behaviour) could lead populations to be innovative or conservative in occupying their potential habitats. Change in spatial distributions could occur because the distribution of potential habitats changed under climate change and or because the population's internal behaviour changed under internal factors such as demographic change.

Theme Session B at the 2006 ASC provided many case study situations around the world where changes in distributions and migrations were observed. In many cases these changes could have been linked to global scale climate features such as the NAO, PDO or ENSO events. However, climate/oceanography links could also be demonstrated at increasingly local levels; from variation in currents e.g. Humbolt, Kuroshio, California and Benguella systems; through location of fronts, e.g. in Baja California, to local vertical structure e.g. off Peru or in the Baltic. Other factors that affected migrations included stock abundance e.g. in Japanese, Californian or S. African sardine, condition factors and spawning e.g. sardinella off W. Africa, and demographic structure e.g. S. African sardine and NSS herring. The conclusion was that while major scale oceanographic features (NAO etc. ocean currents etc.) can be important in setting the context, in many cases very local features and the behaviour and physiology of the fish themselves are also critical factors. Many of the species considered are wide ranging and can tolerate substantial ranges of temperature, so it may be reasonable to conclude that responses to changes in this parameter may not be the only or even the most important factor to consider.

Processes and controls

Habitats and spatial distributions are related but different concepts. Habitats are geographic areas where conditions are suitable in some sense for the fish to occupy these areas. Spatial distributions are the resulting spatial patterns. We therefore discuss separately the controls for the potential suitability of habitats and the controls for the capability of the fish to occupy potentially suitable areas.

The concept of habitat suitability is based on the idea that conditions are appropriate for the realization of a biological function (spawning, feeding, growth, survival). Suitability can be understood to apply to individual fish as in IBM models but also to population fitness as in McCall (1990). Suitability is first governed by physical conditions and lower trophic plankton production associated to these. WKLSTWE (2007) documented environmental conditions in that way in SW Europe. The Workshop continued a series of previous regional GLOBEC workshops focusing on long-term variability in different ecosystems. The joint analysis for multi-annual patterns in 73 time series in climatic, oceanographic, plankton and fish abundance indices demonstrated the impact of climate on ecosystems surrounding the Iberian Peninsula. A clear signal of global change and warming was indicated since 1950s. Also, a major shift in all indices was identified in the late 1970s. A conceptual diagram describing a cascade of processes between climate, foodweb and fish abundance was suggested. Climate drove the balance between upwelling and stratification processes and their seasonal timing, which resulted in periods of particular oceanic regimes that were suitable to particular pelagic species (sardine, mackerel, anchovy), resulting in favouring some of them only during those periods. Regime shifts in oceanic and plankton production has also been documented in the North Sea (e.g. Beaugrand *et al.*, 2001) and the Baltic Sea (e.g. Mackenzie and Köster, 2004). Another work was to characterize potential spawning conditions for anchovy and sardine around the Iberian Peninsula and in Biscay from Gibraltar to Brest (SGRESP 2005, 2006, EU project SARDYN). Based on hydrological (temperature, salinity, stratification) and egg presence survey data, the conditions suitable for spawning were mapped: potential spawning habitats for sardine were less constrained than for anchovy, which were more dependent on high temperature, river plumes and water column stratification.

Though habitats may be potentially suitable, their occupation relies on the ability of the fish to colonize them. Population status and behaviour are key controls of the capability to occupy potentially suitable habitats. SGRESP (2006) formulated the Entrainment hypothesis (also detailed in ICES CM 2006/B:07). Entrainment is a behavioural mechanism based on fish learning from other fish to ensure that migration routes and habitat occupation are maintained over generations. It can explain conservatism as well as changes in life cycle patterns. WKTEST (2007) screened 11 case study populations around the world of herring, sardine, whiting, anchovy, bluefin tuna, white perch and striped bass to support or contradict the Entrainment hypothesis. The work was based on historical patterns in demography, abundance, spatial patterns and within stock diversity. There was evidence of entrainment in all the case studies. Entrainment could occur at any time in the life of a fish and for any type of migration. Major changes in life cycle spatial patterns were related to major changes in abundance and in the proportion of naive to experienced fish as seen in herring populations (Norway, Canada, North Sea) and sardine (California). Entrainment was demonstrated in herring (Canada) by showing crossover of individuals between spring- and autumn-spawning contingents. All stocks showed internal structure and within-population life cycle diversity. Entrainment complemented existing theories on within population life cycle diversity (e.g. partial migration, density-dependent habitat selection) as it could behaviourally overlay deterministic causes and thus reinforce life cycle diversity. There are population consequences of entrainment. Entrainment could act as a low pass filter in the response of populations to climate variation. Because entrainment develops conservatism in habitat use, the occupancy of particular habitats could continue over the life time of several fish generations, although the suitability of these habitats had become suboptimal. This was observed for feeding grounds of herring in the North Sea. Entrainment could generate non-linear effects in the response of populations to fishing. For example, the interaction between entrainment and local overexploitation could create the conditions of a vacuum effect of particular contingents in which recruits get entrained into the life cycle of the most dominant contingents, resulting in maintaining some contingents to a low abundance to the benefit of numerically dominant contingents. This effect explained the evolution of the S. African anchovy fishery marked by a geographical shift. In the case studies investigated (Californian sardine, herring in the North Sea, Norway and Canada) stock collapse was associated with spatial memory collapse and contingent diversity collapse. Recovery of populations to historical abundances and recovery of historical habitats may take much longer than forecasted by models that ignore sub-population structure and behavioural processes.

SGRESP (2006) reviewed process models of fish spatial distributions. Another important process to consider is the density-dependence in the selection of habitats. Based on the ideal free distribution, McCall (1990) developed the basin model for fish spatial distributions. Because of intraspecific competition, when fish density on the most suitable habitats increases, less suitable habitats may become interesting to occupy as they would provide similar suitability per capita. Therefore, diffusion is expected from core to secondary suitable habitats at high abundance levels, making the spatial distribution pattern density-dependent.

Patterns in fish distribution changes are also considered at species level as for example the expansion of southern like species to northern latitudes under presumed climate change. Changes in the distribution of species involve changes in the spatial organization of their life cycles and thus the colonization of novel habitats. WGLESP (2007) investigated whether the expansion of species is due to habitat colonization by recruits or adult fish. The expansion of anchovy and red mullet in the North Sea was analysed using spatial patterns and length distribution in survey data. There was some evidence that the expansion of anchovy was related to repeated good recruitments in recent years, the adult population being sympatric and in a relict state. The summer hydrographic conditions in the North Sea were suitable for anchovy spawning as suggested by a potential spawning model for anchovy. In contrast, there was some evidence that the expansion of red mullet was related to adult fish movements coming from the Eastern English Channel. Both species have now installed life cycles in the North Sea as suggested by the seasonal patterns in their spatial distributions.

Blue whiting in the Barents Sea represents another case (Heino *et al.* 2008). The Barents Sea is the northeastern fringe of the distribution of the species. Fluctuations in distribution and abundance of blue whiting in that area have been marked and two hypotheses were put forward to explain these fluctuations. Recent fluctuations in abundance seemed primarily driven by changes in recruitment of the main NE Atlantic blue whiting population. Strong year classes were particularly abundant in the Barents Sea, which may suggest density-dependent spacing behaviour. However, also oceanographic conditions played a role, because more recruits entered the Barents Sea when inflow of the Atlantic water was high.

Predictive Tools

Models of fish distributions and life cycles are useful to predict changes in spatial distributions under hydro-climate scenarios as well as to disentangle interacting causes when interpreting observed spatial patterns. Habitat suitability is best characterized using a model for the fish biological function under consideration that is applied to input environmental parameters, therefore the importance of these models. Past activity has mainly focuses on statistical models and to a lesser extent on process complex models.

Statistical models are generally data driven and fitted to explain fish presence or density as a function of environmental indices, which are chosen to characterize particular aspects of the habitats. In a regression framework, indices can be constructed to characterize external factors (environmental suitable conditions) and internal factors to the population such as population abundance or age structure. Rindorf and Lewy (2006) constructed explanatory variables related to the population structure to explain the spatial distribution of recruit cod as a function of the distribution of older cod some years before. As already stated above WGLESP (2007) investigated whether suitable conditions for spawning existed in the North Sea in recent years. For that purpose a statistical potential spawning model fitted on data in Biscay that predicted anchovy egg presence as a function of hydrological condition (see SGRESP 2005, 2006) was used to predict anchovy spawning with hydrological conditions in the North Sea. The answer was that potential spawning windows had opened since the late 1990s, which were characterized by high summer temperature and stratification on the German Bight. In effect, anchovy and sardine eggs have recently been observed in ichtyoplankton tows in similar locations than in the 1950s (Alheit *et al.*, 2007).

To better characterize habitat suitability, indices of mesoscale oceanographic features are useful. Long-term indices of ocean climate are generally based on large-scale features (e.g. NAO). Such indices are limited in providing insight on the possible response of fish because the scale of the physical processes described is far greater than the scale at which fish behaviour is understood. Meso-scale oceanographic structures (e.g. fronts, eddies) of tens to few hundred nautical miles and few weeks to months are known to be determinant of biological production, concentration and retention/transport (termed 'the fundamental triad' by Bakun, 1996). Therefore mesoscale oceanographic structures constitute structures of particular importance for the timing and location of key life cycle events in fish populations. WKIMS (2006) documented methods to extract indices of mesoscale structures from satellite images and three-dimensional hydrodynamic model outputs. Based on such procedures, series of mesoscale features are expected to be produced routinely as operational oceanography products, which could lead to construct maps of indices of habitat suitability.

Theme Session G at the 2007 ASC reviewed how to link biological processes to physical features through mechanistic, stochastic and behavioural processes. The primary role of physical variables in structuring the ecosystem was demonstrated in the Baltic by showing how the vertical structure of temperature, salinity and oxygen controls the vertical distribution of zooplankton, sprat and cod. The increasing maturity of three-dimensional ecosystem models was displayed. Modelling studies of the North Sea demonstrated the ability to integrate the system from nutrients to larval fish (sprat and cod). It was also demonstrated that relationships between atmospheric forcing and the lower trophic levels requires explicit consideration of space and time as the different areas of the North Sea have different responses to the atmospheric and oceanic forcing. The use of new technology in field studies was illustrated by the use of acoustic tags to track fish and whales to show how movements and distributions are related to the physical characteristics of the environment and by the use of genetic studies to demonstrate that oceanic fronts can limit gene flow among fish populations. Laboratory studies showed that turbidity and patchiness, which are not generally accounted for in three-dimensional ecosystem models, can have a substantial impact on an organism's ability to find food. One of the goals of linking physical oceanographic features with biological production and fish habitat is to develop quantifiable relationships that can be used to create predictive habitat maps. Several studies attempted to find explicit relationships between the physical environment (e.g. depth, water temperature, bottom type) and fish distributions. The efforts lead to mixed results. Linkage between biology and physics were best identified at relative small-scale. Inter-annual variations may contain processes involving larger scales. Behaviour and animal movement were identified as key for building the capacity to pass from small-scale to larger scale.

Future directions within ICES for further developing predictive tools include:

- The monitoring of habitat suitability using operational oceanographic products;
- The prediction of successful spawning windows in space and time under different climate scenarios using three-dimensional biophysical larvae IBMs;
- The prediction of fish growth and reproductive potential under different climate scenarios using bioenergetic models forced by three-dimensional ecosystem model outputs;
- The integration of behavioural processes in models of fish spatial distributions to predict the effective occupation of potentially suitable habitats.

Further, coupling full life cycle fish models to lower trophic ecosystem models is becoming the state-of-the-art (e.g. Werner *et al.* 2001; Megrey *et al.*, 2007; Werner *et al.*, 2007) allowing integrating the many controls of all life cycle events. Coupled hydrodynamics and biological models (e.g. Nutrient – Phytoplankton – Zooplankton models, bioenergetics models, Individual Based Models) are currently being developed and applied in different parts of the world. Within ICES collaboration between the Oceanography and Living Resources Committees is essential to the multidisciplinary development of these future directions.

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3 ToR c) Report new results and methods for modelling habitat occupation

A review on habitat concepts and modelling are here reported.

Habitat characteristics and their modelling

Habitats and spatial distributions are related but different concepts. Habitats are geographic areas where conditions are suitable in some sense for the fish to occupy these areas. Though habitats may be potentially suitable, their occupation relies on the ability of the fish to colonize them. Population sub-structure and behaviour are key controls of the capability to occupy potentially suitable habitats. External factors to the population that define potential suitability need be distinguished from internal factors which define the conditions for effective use of the potentials. Spatial distributions result from the interaction between external environmental forcing and internal population factors. Descriptive, statistical and mechanistical approaches to monitor and predict different characteristics of habitats are presented below.

Habitats are often referred to using particular terminology, e.g. potential, suitable, essential habitat. A glossary of characteristics was defined and for each a method associated for its estimation (Table 1). Potential habitats correspond to environmental conditions that are (physiologically) necessary for the fish to be present. Statistical models of potential spawning habitats were developed based on egg survey data and environmental condition. The models predicted egg presence given the hydrological and geographic indices (Planque *et al.*, 2007; Bernal *et al.*, 2007). Potential habitats can also be estimated using first principals and mechanistic approaches. Preferred habitats define the necessary conditions for high fish concentration to happen. Here again statistical tools can be used: regression quantile (Koenker, 2005), quotient plots (van der Lingen *et al.*, 2004; Bernal *et al.*, 2007), regression using positive values only. Habitat suitability refers to conditions that support a particular biological function (growth, spawning). Modelling habitat suitability requires mechanistic models such as bioenergetic models. Using a Dynamic Energy Budget Model (DEB), different areas in the Bay of Biscay were investigated for their potential to be suitable for anchovy growth and reproduction in different seasons and for different anchovy length sizes (Pecquerie, 2007). Essential habitats define areas that are crucially important for population viability. Essential habitats were evidenced using spatialized population matrix models and elasticity analysis (Vaz and Petitgas, 2002). Realised habitats are the parts of the potential habitats effectively occupied in each year. Modelling realized habitats requires either mechanistic models or statistical analysis. The statistical approach of empirical orthogonal functions (EOF) was here useful (Petitgas, 2008) to formulate interannual change as a change in the combination of principal patterns. In all, habitat models are useful tools in a climate change context for explaining past patterns as well as making predictions based on environmental scenarios.

Table 1. Glossary of habitat characteristics with definition and estimation methods.

Terminology	Definition	Estimation Method
Potential habitat	Necessary conditions (physiology)	GAM applied to 0/1 data Physilogical tolerance
Preferred habitat	Necessary conditions for high concentrations	Quotient plots Cumulative functions GAM (0/1 data) * GAM (pres.only data) Quantile regression
Realised habitat	Part of the potential effectively occupied	Empirical Orthogonal Functions (EOF)
Suitable habitat	Conditions supporting a biological function (e.g. growth, spawning)	Individual-based bioenergetic model
Essential habitat	Key area for population viability	Spatialized matrix population model

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Modelling habitats statistically

This section summarizes different aspects of statistical habitat modelling that were presented during the summer school on 'Habitat modelling of Marine Populations', held in Lisbon (Portugal), 2-13 July 2007.

Habitat models (Guisan & Zimmermann, 2000), habitat suitability models (Hirzel *et al.*, 2006) and species distribution models (Guisan & Thuillier, 2005) are similar in that they are constructed by relating observed biological response to environmental factors using a statistical model that is calibrated and evaluated. Calibration consists in choosing the most adapted environmental factors and measuring the goodness fit of the model. The topic of habitat modelling is large considering the diversity in biological response and environmental factors as well as modelling, calibration and evaluation techniques.

Austin (2002; 2007) highlights main characteristics of biological responses and environmental factors. Both can come from direct (field survey, experiments, collection data) or indirect (remote sensing, outputs of physical models) measurements. Data for the biological responses can be qualitative data (presence, presence pseudo-absence, presence absence) and/or quantitative data (counts, abundances, recruitment). Environmental factors can be classified into three main categories: 1) resource covariate indicating a resource consumed by the species (silicate, nitrates, phytoplankton…), 2) direct covariate, which potentially has an physiological impact on the species but that is not consumable (temperature, salinity, pH), 3) indirect covariate, which does not act directly on the species (latitude, longitude, altitude, depth). Resource and direct effects can also be named proximal and indirect effects distal. For example, chlorophyll a, as a phytoplankton indicator, can be considered as a resource and a proximal factor for copepods but as a distal factor for zooplanktivorous fish. Choice among the environmental factors is usually a compromise between known relationships and availability of the data. Whereas the model should be better if only resources and proximal factors are used, they are not always available. Indirect factors, often considered as a mix of direct and proximal effects, are usually taken in place of resources and direct effects in habitat model because these are easier to collect at a large-scale of space and time. Values of the biological response with their corresponding values of environmental variables constitute the main dataset. Depending of the size of this dataset, it is usually split in two, one for calibration and the other for evaluation of the model.

Numerous statistical methods already exist (Guisan *et al.*, 2006). Choice of the most adapted one depends on two main points: 1) assumptions on the link between the response and the environmental factors (shape, mean or maximum response, presence of a limiting factor) and 2) the type of the biological response. Usually, the environmental gradient that is measured is not large enough to have the entire biological response of the species and a linear model is sufficient. However, according to the continuum theory (Oksanen & Minchin, 2002) and the ecological niche theory (Chase & Leibold, 2003), a linear response is not always adapted. The response shape can be model driven (linear or polynomial) like in Generalised Linear Models (GLM, McCullagh & Nelder, 1989) or data driven with a smoothed response like in Generalised Additive Models (GAM, Hastie & Tibshirani, 1990; Wood, 2006). The smooth can be fit using the derivates, as in Multi Adaptive Regression Splines (MARS, Leathwick *et al.*, 2005), Generalised Regression Analysis and Spatial Prediction (GRASP, Lehman *et al.*, 2002) and Hyperniche (McCune, 2006). All these methods model a mean response along an environmental gradient. Cade *et al.* (1999) and Hiddink (2005) recommend modelling the maximum response so as to take into account limiting factors not in the model and Liebig's Law of minimum theory. Quantile regression techniques (QR) were developed for that purpose. For presence only data (Pearce & Boyce, 2006 ; Hirzel *et al.*, 2006), climatic envelop methods (Pearson & Dawson, 2003) such as BIOCLIM, HABITAT, DOMAIN, Support Vector Machines (Guo *et al.*, 2005 ; Drake *et al.*, 2006) and Ecological Niche Factor Analyses (Hirzel *et al.*, 2002) can be used. For presence-absence data, GLM, Generalised Equation Modelling, GAM and Boosted Regression Trees are available. For continuous data, GLM, GAM, QR Artificial Neural Network, Classification and Regression Trees are now standard methods (Thuillier, 2003). Guisan *et al.*, (2006) and Austin, (2007) highlight that many other methods are under development such as Maxent, Canonical Gaussian Ordination, Structural Equation Modelling, Generalised Dissimilarity Models and Geographical Weighted Regression. All these methods are available in the form of R packages (http://www.r-project.org/). A rich and recent literature on comparing all these techniques is also available (Thuillier, 2003; Segurado & Araujo, 2004; Elith *et al.*, 2006; Maggini *et al.*, 2006; Moisen *et al.*, 2006; Moisen & Frescino, 2002; Leathwick *et al.*, 2006).

Calibration corresponds to model fitting on observed data. Differences between observed and fitted responses are quantified using the deviance. Several models can be computed and the model with the smallest deviance chosen as that with the best fitted. The recommended approach to model building is that based on criteria for selecting covariates (Burnham & Anderson, 2002). This approach applies the principle of parsimony by keeping the minimum necessary number of environmental factors needed to have the most powerful predictive ability of the model. As a predictive ability measure, a selection criterion used can be the deviance penalised by the number of observation and environmental factors included in the model. Even if several criteria are available, Akaike Information Criterion (AIC) is the most used. The most parsimonious model is the one with the lowest AIC, indicating the best compromise between the predictive power and the number of environmental factors included in the model.

Evaluation of the model consists in applying the model on a dataset that has not been used for model fitting and comparing predicted response values with observed response values. If there is not enough data, the model is evaluated on the same dataset as used for the calibration in which case resampling techniques such as boostrap, cross-validation and jackknife are adapted (Guisan & Zimmermann, 2000). The underlying principle of these techniques is to apply the fit the model several time on a subset of the data (different each time) and to compare predicted response with observed response. If possible to split the data in two, evaluation of the model is done on another dataset using Area Under ROC Curves (DeLong *et al.*, 1988) for binary data (Fielding & Bell, 1997; Pearce & Ferrier, 2000) or Spearman and Kendall test (Guisan & Zimmermann, 2000) for continuous data.

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4 ToR d) Liaise with other ICES groups of the Oceanography Committee and suggest ways to collaborate to address hydro-climate forcing on spatial distributions of pelagic fish

In preparing WKSPCLIM, contacts have been made to allow for linking oceanography with fish population responses. Also, the work of WGLESP has been presented to the WG on Physical-Biological Interactions (WGPBI) to envisage modelling the full life cycle of fish using outputs of biogeochemical models. A Theme Session co-promoted by WGLESP and WGPBI is proposed for the ASC in 2010 on modelling the full life cycle of fish (Annex 5). The steering group on climate change SGCC is expected to be a future forum providing guidance on how to make plans on the topic. In that context, small pelagic fish could be taken as indicators of climate change.

Annex 1: List of participants

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Annex 2: Terms of reference for this report

2007/2/LRC13 The ICES/GLOBEC Working Group on Life Cycle and Ecology of Small Pelagic Fish [WGLESP] (Chair: P. Petitgas, France) will meet by correspondence to:

a) prepare a document compiling the knowledge assembled by SGRESP on life cycle patterns and mesoscale oceanographic features for small pelagic fish in the North East Atlantic, to be proposed for publication as a Cooperative Research Report;

b) summarize outcomes from past activity (e.g. SGRESP, OSPAR request, 2006 Theme Session B, 2007 Theme Session G, WKLTVSWE, WKTEST) to document the mechanisms and controls of changes in spatial distributions and migration patterns;

c) report new results and methods for modelling habitat occupation;

d) liaise with other ICES groups of the Oceanography Committee and suggest ways to collaborate to address hydro-climate forcing on spatial distributions of pelagic fish.

WGLESP will report by 1 May 2008 on ToR b) for the attention of WGECO and by 30 June 2008 for the attention of the Living Resources Committee, the Oceanographic Committee and GLOBEC/SPACC on the remaining ToRs.

Annex 3: WGLESP terms of reference for the next meeting

The ICES/GLOBEC Working Group on Life Cycle and Ecology of Small Pelagic Fish [WGLESP] (Chair: P. Petitgas, France) will meet at XXXX (location and date to be confirmed) to:

a) Complete the CRR on life cycle patterns initiated in 2008;

b) Report new results of relevance to LESP, and the impact of climate change

c) Review causes and mechanisms explaining changes in small pelagic fish species occurrence;

d) Building on WKSPCLIM and SGCC work, propose a workplan to envisage small pelagic fish as indicators of climate change.

WGLESP will report by XXXX to the attention of the LRC Committee.

Supporting Information

Priority:	The work of the Group is essential if ICES is to progress the understanding of environmental forcing on life history, spatial and population dynamics of pelagic fish to provide alternative basis to management on stocks recognized to fluctuate under environmental forcing. There is no other group within ICES on this thematics that is also key for recovery plans of depleted stocks.
Scientific justification and relation to action plan:	The purpose of the WG is i) to integrate various data sources and ii) develop understanding of how the spatial dynamics of the biological cycle and the stock dynamics are related to the ecosystem thus increasing ICES ability to use ecological information in assessment and prediction of small pelagics. The WG works on different case studies in the ICES waters and links with GLOBEC and PICES work on similar topics.The WG addresses Goal 1 Understand the physical, chemical, and biological functioning of marine ecosystems, in particular action numbers 1.2.2 Changes in spatio-temporal distributions in relation with environmental change, 1.6 assess and predict impact of climate variability and 1.7 play an active role in collaborations between ICES and other international research such as GLOBEC. This WG is also related to Goal 4 Advise on the sustainable use of living marine resources, in particular action number 4.11 Develop the scientific basis for an ecosystem approach to management.
Resource requirements:	No specific resource requirements beyond the need for members to dedicate time on the workplan of the WG.
Participants:	The Group is normally attended by some 10–15 members and guests.
Secretariat facilities:	None.
Financial:	No financial implications.
Linkages to advisory committees:	Linkage via particular ToRs (e.g. climate change or recruitment scenarios)
Linkages to other committees or groups:	Links with WGPBI, WGFE, WGSAEM, SIMWG and SGCC. Links with groups dealing with environmental and fisheries survey data.
Linkages to other organizations:	This group is acknowledged to be of relevance to the GLOBEC/SPACC programme by its executive committee.

Annex 4: Recommendations

Recommendation	For follow up by:
1. Theme session for 2009 ASC "What do fish learn in schools? Life cycle diversity within populations, mechanisms and consequences". Conveners: D. Secor, P. Petitgas, I. McQuinn, S. Cadrin. Annex 5.	LRC and CONC
2. Theme session for 2010 ASC "Combining models of the full life cycle of fish with lower trophic models: integration and prediction". Conveners: P. Petitgas, B. Megrey, K. Rose. Annex 5.	LRC/OCC and CONC

Annex 5: Theme session proposals

Theme session proposed for the 2009 ASC

What do fish learn in schools? Life cycle diversity within populations, mechanisms and consequences

Conveners: Dave Secor (USA), Pierre Petitgas (France), Ian McQuinn (Canada), Steve Cadrin (USA).

Depleted fish stocks, degraded habitats, and uncertainty in forecasts of future ecosystem states emphasize the need to include the notions of resilience and associated life cycle diversity as objectives for fishery management. Life-cycle diversity within populations and knowledge transfer between generations are increasingly recognized as factors that can influence population resilience and thus fishery and habitat recovery actions. Concepts explaining life cycle diversity within populations and its persistence include genetic polymorphism, partial migration, and social transmission of learned migration behaviour. .Although life- cycle diversity is increasingly recognized as a pattern common across diverse fish taxa, mechanistic studies and concepts explaining this diversity are nascent. Further, relatively little attention has focused on the consequences of this diversity in particular for population resilience, spatial management strategies and recovery plans.

Across marine and diadromous fish, papers are welcome on the following topics:

- life cycle diversity within populations, its persistence and change
- conditional strategies leading to partial migration
- social transmission of habitat use
- population genetic structure and polymorphism
- mechanisms for population resilience
- population-level effects of infra-population diversity
- recovery plans accounting for spatial effects
- spatial management strategies accounting for essential habitats.

Theme session proposed for the 2010 ASC

Combining models of the full life cycle of fish with lower trophic models: integration and prediction

Conveners: Pierre Petitgas (France), Bernard Megrey (USA), Kenneth Rose (USA)

Rationale: The subject is the key to understanding the many controls of population dynamics that occur at various stages in the life history. Mechanistic tools are necessary to increase predictability of changes in fish distribution and productivity under global change scenarios and for fishery management or restoration plans. Some models and applications have already been developed and a first review is timely on this topic of growing scientific interest.

Presentations are welcomed on: bioenergetics models, displacement models and feeding models of the juvenile and adult fish at individual and population levels, as well as on their demonstrative use in applied cases.