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HOW LIFE HISTORY PATTERNS AND DEPTH ZONE ANALYSIS CAN HELP FISHERIES POLICY

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ABSTRACT

The life-history patterns of fish species are complex. But much of this complexity can be captured in simple diagrams of coastal transects, where juveniles usually occur in larger numbers in shallow waters, while adults generally inhabit deeper, offshore waters. Such coastal transects can be used to show how different fisheries sectors (e.g. small versus large scale) may exploit different parts of the life history of the same species or stock. Thus, a species may 'connect' small with large scale fishery sectors through their life history patterns. We show how this can be visualized through iconographic representations of generalized life history patterns and depth profiles, with specific key life-history parameters. Relevant patterns include spawning areas, nursery/juvenile distributions, adult distributions and spawning migrations. Four preliminary case studies presented here illustrate some general patterns with regard to water depth and distance from shore. The diagrams allow us to incorporate into management the concept of life history interconnectivity between different fishery sectors. This contributes to sustainable ecosystem-based approaches by informing policy options when faced with decisions to rationalize overcapitalized fisheries.

INTRODUCTION

The stock of an exploited species may be utilized by more than one fisheries sector (such as inshore, small-scale fisheries and offshore, large-scale fisheries) during different stages in the species life history (see Ruttan et al. 2000). Life history patterns are generally viewed as multi-dimensional in scale, with complex interactions between components defined by ecology, oceanography, time and geography. Often this complexity has made it difficult to assimilate potential effects of multiple fishery sectors on a species and the industry it supports. This may be either due to the perception of multi-dimensional complexity thought to be intractable, or because of an oversight of basic patterns.

Here, we argue that this multi-dimensional complexity can be reduced to a simpler, generalized two-dimensional life history pattern, while still capturing the essential information. Both Charles Darwin and Alexander von Humboldt used the method of reduced dimensionality to focus one's attention to the key issues while capturing most of the significant information concerning the topic at hand. For example, after reviewing much literature, Darwin concluded that "latitude is a more important element than longitude" for explaining the distribution of organisms (Barrett et al. 1987). This concept has recently been revisited in a latitudinal analysis of population dynamics and ecology of flatfishes (Pauly 1994). It was Humboldt, however, who in his classic *Voyage aux régions équinoxiales du Nouveau Continent* first used a transect technique to visualize the advantage of reduced dimensionality in explaining observed patterns in distribution (Gayet p. 2284-2287 in Tort 1996). In fisheries science, a classic example of data suitable for reduced dimensionality was presented by Garstang (1909) for the North Sea plaice (*Pleuronectes platessa*, Figure 1). Heincke (1913) re-expressed this as a 'law' wherein size increases with distance from shore (and depth), while numbers declined.

The life history characteristics of many species and stocks show generalized two-dimensional patterns, involving water depth and/or distance from shore. Pauly (1982) indicated such a pattern for a tropical bay and mangrove estuary, and FAO (1972) used this approach for many species in their *Atlas of the Living Resources of the Seas*. It is recognized that for many applications an inshore/offshore axis may better convey information on structure and processes than an alongshore axis or general geographic map view (Pauly and Lightfoot 1992). A good example of this is demonstrated by comparison of Garstang's map-view of plaice size distribution in the North Sea (Figure 1) with our representation of the same information for the same species and area (Figure 5). Such a transect approach permits the use of icons to represent key processes or patterns, as well as standardization of axis (e.g. log scale), which enables most species or stocks to be directly compared across extensive depth and distance scales.

The visualization of two-dimensional life history patterns is clearly only a small part in our evaluation of ecosystem effects of fishing (see Pauly and Pitcher 2000). Other components of the *Sea Around Us Project* assess the yield as well as economic benefits gained and foregone through non-optimal stock use by each fisheries sector (small scale versus large scale, incorporating gear type, vessel size and area of operation) for each area in the North Atlantic (see Ruttan et al. 2000, Munro and Sumaila 2000). We will be super-imposing the various scales of operation (depth of fishing and distance from shore) of each fisheries sector onto the life history illustrations of each species concerned. Thus, by utilizing standardized graphical illustrations in conjunction with a presentation of existing (or potential) 'life history/fisheries integration' problems, we hope to provide some additional impetus, as well as visual clarity, to future policy and management decisions, particularly with regards to rationalization of over-capitalized fisheries.

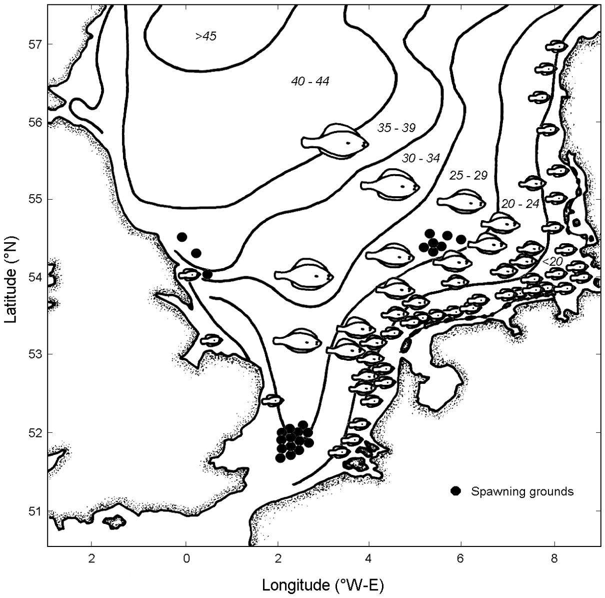

Figure 1. Schematic representation (geographic map view) of the distribution of plaice (*Pleuronectes platessa*) in the North Sea. Mean sizes (cm TL) are given for each depth isobar (modified after Garstang 1909).

It might be questioned why we chose iconographic visualization as our preferred vehicle to present these patterns and the message associated with them? A clear advantage of standardized, two-dimensional graphs is that they permit comparison between different examples at one glance (Pauly and Lightfoot 1992). Tufte (1983) suggested that: "...of all methods for analyzing and communicating information, well-designed data graphics are usually the simplest and at the time the most powerful. Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency." According to Tufte (1983), graphical displays should:

- "Show the data
- Induce the viewer to think about the substance rather than about methodology or graphic design
- Encourage the eye to compare different pieces of data
- Avoid distorting what the data have to say
- Give the viewer the greatest number of ideas in the shortest time with the least ink in the smallest space."

Adhering to this theory of information presentation, our graphs are designed to be easy to decode (incorporating hues chosen to permit easy decoding by color deficient viewers, Tufte 1983 p. 183), contain key information (four major life history segments) and are standardized in scale, to permit direct comparison between species and areas.

The distance from the coast (and depth) of major population components determines their relative vulnerability to small-scale (often coastal) and large-scale (often offshore) gear and hence the existence and intensity of interactions and (potential) conflicts between these different fishery sectors. We anticipate that the final product (including the superimposed scales of operation of various fishery sectors, see Ruttan et al. 2000) will provide visual clarity on how separate fishery sectors act simultaneously on the same stock through their spatial and gear-selective fishing effort on different key life history stages. Furthermore, the depth distribution patterns will help us assign catch data assimilated by the project to the areas of the marine ecosystem classification to be used by this project. Thus, appropriate transects may be generated, if necessary, for different stocks with regards to the specific marine ecosystems as defined for the *Sea Around Us Project* (see Pauly et al. 2000).

METHODS

The species and stock specific data summarized in the coastal transects were obtained through standard literature searches, as well as species specific searches of FishBase (www.fishbase.org). The information for the Barents Sea deepwater redfish (*Sebastes mentella*) stock was augmented through a personal communication from Dr.

Konstantin Drevetnyak at the Russian Polar Institute in Murmansk, Russia.

The depth transects were obtained from ground-truthed depth data (standardized to Mean Sea Level; P. Sloss, NOAA-NGDC, pers. com.) with a two-nautical mile resolution based on satellite sources ('Global Relief' NOAA-NGDC, MGG Division, Boulder, Colorado,USA). The depth contour data was used in the *Surfer* geo-statistical program to calculate depth contours between locations relating to the general geographic area being considered. Thus, individual bottom contour transects represent typical depth contour transects derived from the stock specific geographic area. Graphs are standardized to log-scales to permit most species and stocks to be directly comparable across extensive depth (1-10,000 m) and distance scales (0.1-1,000 km), while simultaneously permitting shallow water, near-shore recreational fisheries sectors to be represented where applicable.

Four key life history stages are being used: Larval dispersal indicated by black dotted arrows (from hatching or larval extrusion to settlement or early juvenile stage), juvenile stages in blue (from post-larval to pre-fishery-recruitment stages), adult stage in brown (recruited to fishery) and spawning depth strata in red (representing depth zones used preferentially for spawning). Additional arrows indicate ontogenetic movements (blue) and regular spawning migrations (brown). The larval stage is being represented as a flow arrow only, to illustrate the link, via larval stage, between spawning areas and juvenile nursery habitats.

CASE STUDIES

In this paper we present four species as case studies, i.e., Atlantic herring (*Clupea harengus*), North Sea plaice (*Pleuronectes platessa*), Atlantic cod (*Gadus morhua*) and deepwater redfish (*Sebastes mentella*), each of which is associated with important fisheries and ecosystems of the North Atlantic.

Species with inshore / offshore patterns

Atlantic herring

Herring populations (*Clupea harengus*) often display complex feeding and spawning migrations (Iles 1971). They are separated into numerous local 'races', often identified by spawning locations and spawning periods (e.g. North Sea spring spawning herring; Muus and Dahlstrøm 1977, McKeown 1984, Blaxter 1985). Areas suitable for spawning by herring are banks and coastal areas with stony and rocky bottom and depths less than 250 m (Runnstrøm 1941a and Dragesund 1970 in Slotte and Fiksen 2000). Herring eggs are demersal (Blaxter 1985) and larval duration range from 2-6 months depending on stock (Houde and Zastrow 1993, FishBase 1999, M. Sinclair, pers. com.). Research on herring life history indicates that in many cases there is considerable mixing both in the nursery areas and feeding grounds of many stocks or 'races', while segregation occurs during spawning and early larval stages (Iles 1971, Iles and Sinclair 1982, Sinclair and Iles 1985, Sinclair et al. 1985).

Arcto-Scandian/Norwegian Spring Spawning herring stock (Figures 2 and 3)

Historically (i.e. pre-1970s, Figure 2), the Arcto-Scandian herring stock displayed extensive seasonal and ontogentic migrations. Spawning areas are along the south-western and western Norwegian coast, juvenile nursery areas are primarily in the Barents Sea, and adult feeding and over-wintering areas are offshore as far as Faroe Islands, Jan Meyers Island and Iceland (FAO 1972 maps 2.2 and B.2, Muus and Dahlstrøm 1977, Slotte and Fiksen 2000).

In recent years the Norwegian Spring Spawning herring stock (formerly called Arcto-Scandian stock) has recovered from near extinction in the late 1960s early 1970s, and appears to have re-established its previous patterns (Figure 2). For nearly 25 years after the collapse, the oceanic (Barents Sea, Iceland and Norwegian sea) nursery, feeding and wintering areas were abandoned, and the entire life cycle was spent in Norwegian coastal waters and fjords (Figure 3, Dragesund et al. 1980, Holst et al. 1998, Rottingen 1990, Hamre 1990 in Slotte and Fiksen 2000). During the 1990s, the feeding area has again expanded westwards to the Norwegian Sea (Holst et al. 1998, Slotte and Fiksen 2000), which is indicative of a return to the pattern illustrated in Figure 2. Herring larvae drift to a variety of nursery grounds in coastal fjords and the Barents Sea, and mix as adults on selected spawning grounds irrespective of nursery origin.

North Sea herring stocks (Figure 4)

The North Sea stock has generally been sub-divided into three groups, the northern North Sea summer-spawning, the central North Sea autumn-spawning and the Southern Bight winter-spawning groups (McKeown 1984). Depth-related generalized life history patterns are very similar for all three groups. Here, the Southern Bight winter-spawning group is illustrated as representative (Figure 4). Juveniles spend their early life in shallow, inshore areas. Once they reach approximately 10 cm in size, they move further offshore into deeper waters mainly to the south and east of Dogger Bank in the southern North Sea. Sexually immature but larger fish generally move further north and feed in the northern part of the North Sea. Adults migrate between the southern spawning area and northern feeding areas on an annual basis (McKeown 1984 and references therein).

Plaice (Figure 5)

The Plaice (*Pleuronectes platessa*) is a right-eyed flatfish occurring commonly in the North East Atlantic (Garstang 1909, McKeown 1984, FishBase 1999). In the North Sea four major spawning subgroups are recognized: Scottish east coast, Flamborough, Southern Bight and German Bight spawning group (McKeown 1984 and references therein). They spawn in 25-75 m depth, eggs and larvae are pelagic for approximately 3-8 weeks, and metamorphose to juveniles which settle in nursery areas in shallow, coastal waters (Muus and Dahlstrøm 1977, McKeown 1984, Figure 5). Juveniles remain in shallow waters (<20 m) for the first few years, then start moving into deeper waters. Plaice reach sexual maturity at 3-4 years, then undertake their first migration to spawning areas. Thereafter they disperse over a larger area, mainly in deeper waters, with overlap with other plaice stocks (McKeown 1984).

Atlantic Cod (Figures 6 and 7)

The Atlantic cod (*Gadus morhua*) is generally a diurnally schooling, demersal or benthopelagic species, occurring from shoreline to 500-600 m depth (FAO 1972 map B.1, Muus and Dahlstrøm 1977, Cohen et al. 1990, FishBase 1999). It can undertake long-distance migrations (FAO 1972 map 2.1, Cohen et al. 1990). Spawning takes place in 50-150 m depth for Barents Sea stock (Mukhina et al. 1995, Figure 6) and Gulf of Main/Georges Bank stocks (Serchuk et al. 1994, Figure 7). During the spawning season adults are highly aggregated and closely associated with banks or shelf-edge features (spawning areas), whereas during the non-spawning season distribution is more widely dispersed (Frank et al. 1994). Cod eggs are pelagic and concentrate in the 0-10 m depth strata , larvae hatch within 2-4 weeks of spawning, and settlement occurs after 3-5 months at 3-6 cm in size (Muus and Dahlstrøm 1977). Historically, sexual maturity was reached at between 4-15 years, however, presently this is reduced to 1-7 years due to overfishing (Serchuk et al. 1994, Longhurst 1998). Historic longevity was approximately 25 years, maximum size ~200 cm (Muus and Dahlstrøm 1977). Cod in northern Norway (Figure 6) are considered as two entities, although managed as a single stock: Norwegian Coastal Cod and Barents Sea stock (Fyhn et al. 1994, Loken et al. 1994). Loken et al. (1994) compared Barents Sea cod with Coastal Cod stocks in Norway, and found different early life histories, but no conclusive indication of different stock structure. Barents Sea cod juveniles remain planktonic for longer and settle far to the north and east in the Barents Sea (McKeown 1984, Helle 1994, Loken et al. 1994), while coastal cod juveniles settle earlier in very shallow coastal waters where the macroalgal belt might provide protection from predation (Loken et al. 1994). Similar shallow water settlement is also observed in North Sea cod (Riley and Parnell 1984 in Loken et al. 1994). Juvenile cod (1-year-old) have been reported to inhabit the shore slope of fjords between 10-30 m depth (Svendsen 1995). In the western Atlantic (e.g. Georges Bank, Figure 7), as well as on other shelf areas, most cod larvae appear to be retained on the banks used as spawning areas due to hydrodynamic patterns (Anderson et al. 1995) and the early stage of larval activity assisting movements shoalwards (Serchuk et al. 1994). Coastal cod within the Gulf of Maine (Figure 7) appear to maintain their own spawning grounds (e.g. Sheepscot Bay), and show an affinity to shallower (< 100m) coastal areas (Perkins et al. 1997).

Species with offshore pattern only

Deep water redfish (Figures 8 and 9)

In the North Atlantic there are two main species of redfish, *Sebastes mentella* (deepwater redfish, ocean perch) and *S. marinus* (golden redfish), which overlap in occurrence (FAO 1972 map A.1, Christensen and Pedersen 1989). A third species (*S. viviparus*) is generally found in shallower waters, and is the most common redfish in the North Sea and the Skagerrak (Anon. 1998).

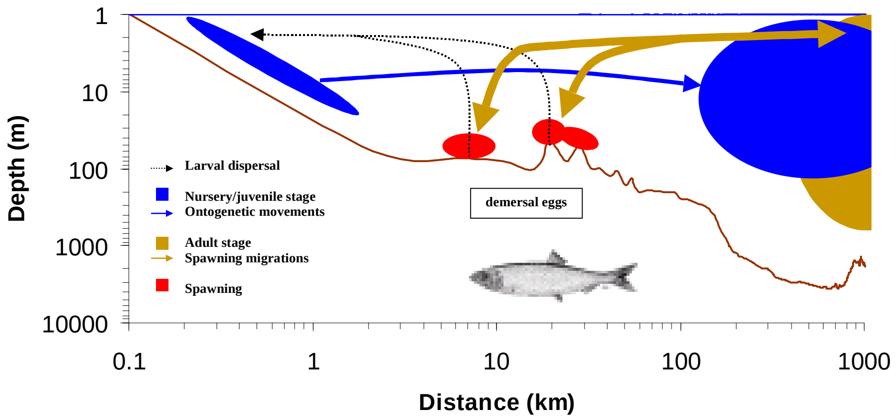

Figure 2. Generalized life history pattern by depth zone for Norwegian Spring Spawning herring (*Clupea harengus*) prior to the stock collapse in the late 1960s early 1970s, and the currently re-established pattern. Brown line represents typical depth transect from approx. 63°N, 8°E to 67°N, 11°W.

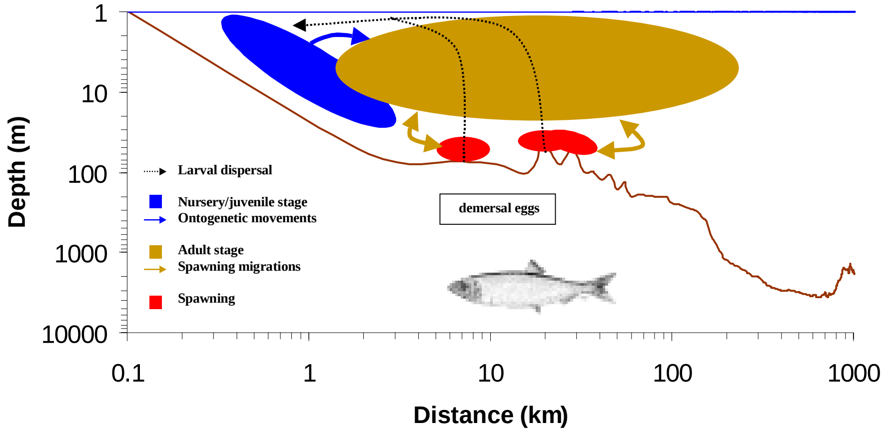

Figure 3. Generalized life history pattern by depth zone for Norwegian Spring Spawning herring (*Clupea harengus*) representative of the 25 years after the stock collapse in the late 1960s early 1970s. Brown line represents typical depth transect from approx. 63°N, 8°E to 67°N, 11°W.

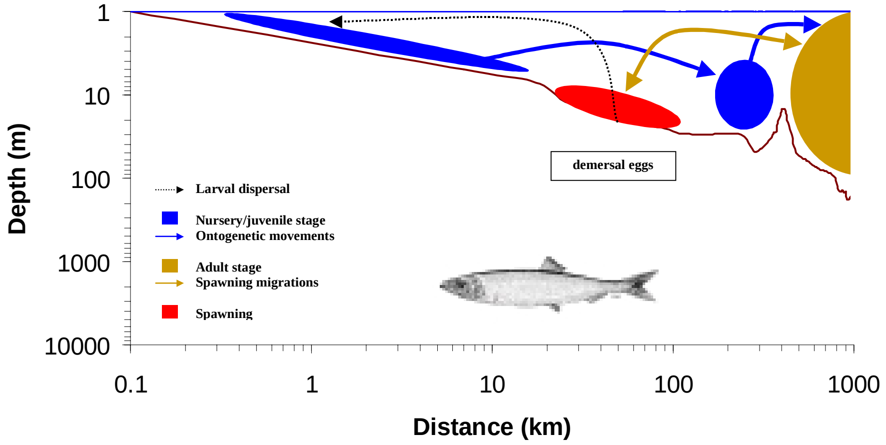

Figure 4. Generalized life history pattern by depth zone for Southern Bight winter spawning herring in the North Sea (*Clupea harengus*). Brown line represents typical depth transect from approx. 51°N, 3°E to 63°N, 2°E.

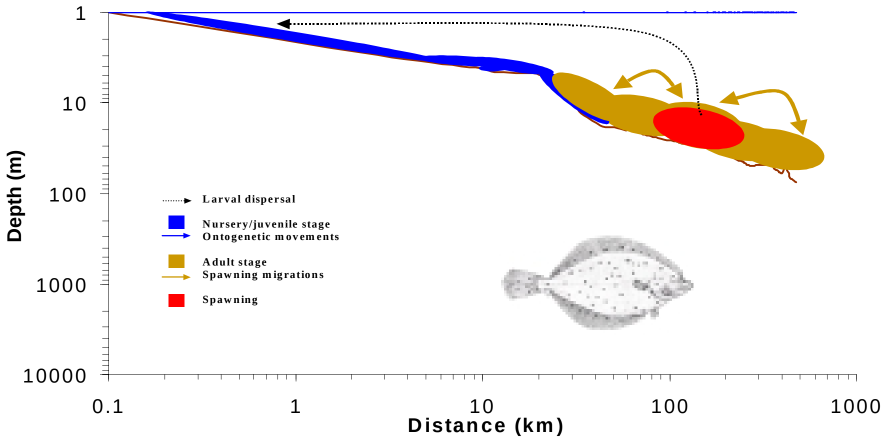

Figure 5. Generalized life history pattern by depth zone for North Sea plaice (*Pleuronectes platessa*). Brown line represents typical depth transect from approx. 53°N, 8°E to 56°N, 3°E.

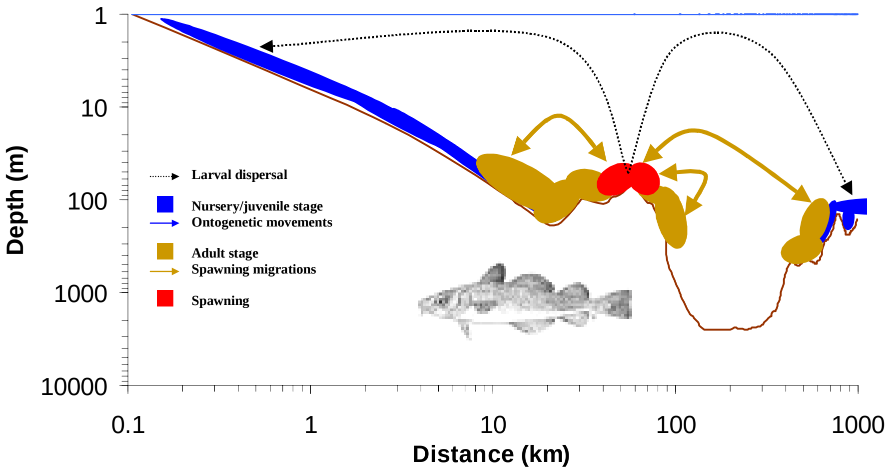

Figure 6. Generalized life history pattern by depth zone for Barents Sea and Norwegian Coastal Cod (*Gadus morhua*). Brown line represents typical depth transect from approx. 68°N, 13°E to 76°N, 18.°E.

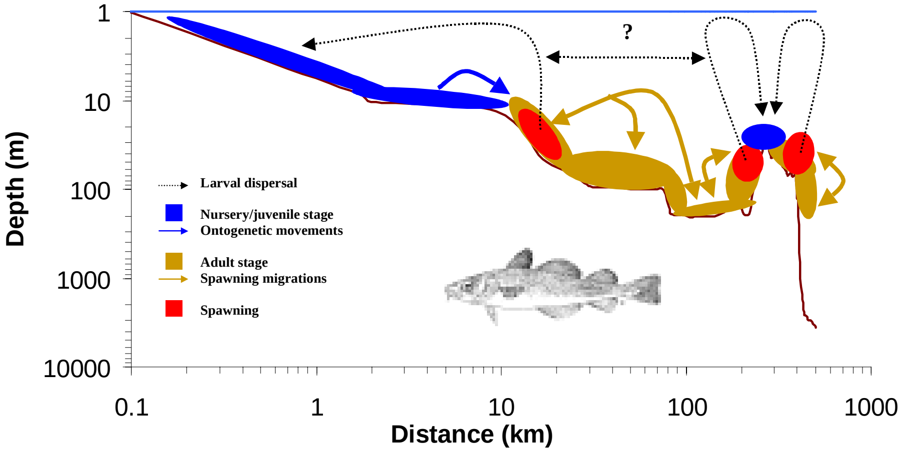

Figure 7. Generalized life history pattern by depth zone for Gulf of Maine and Georges Bank cod stocks (*Gadus morhua*). Brown line represents typical depth transect from approx. 42°N, 70°W to 40°N, 65°W.

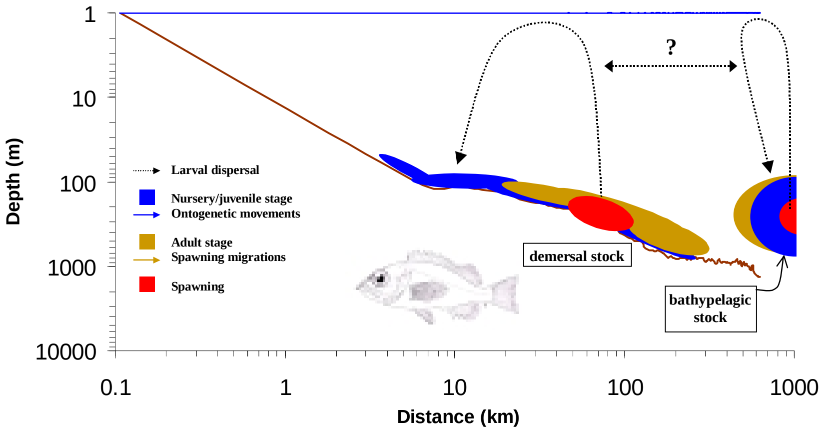

Figure 8. Generalized life history pattern by depth zone for Irminger Sea deepwater redfish stocks (benthic and mesopelagic *Sebastes mentella*). Brown line represents typical depth transect from approx. 63°N, 22°W to 59°N, 30°W.

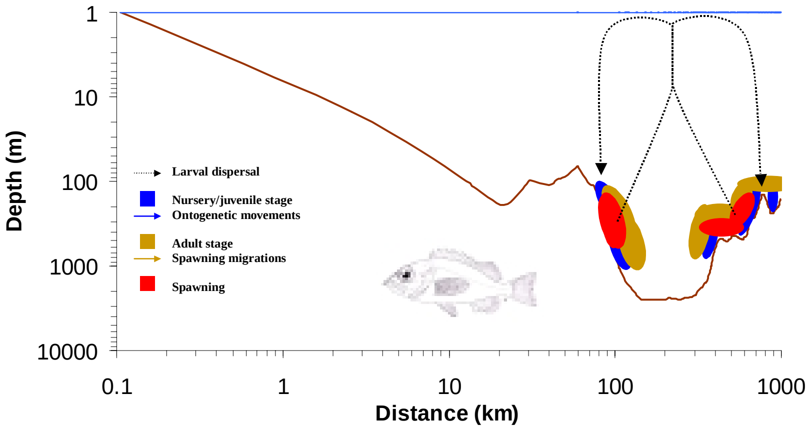

Figure 9. Generalized life history pattern by depth zone for Barents Sea deepwater redfish (*Sebastes mentella*). Brown line represents typical depth transect from approx. 68°N, 13°E to 76°N, 18°E.

Similarly, a third species (*S. fasciatus*, Ascadian redfish) occurs in the western Atlantic, also primarily in shallow waters in inshore areas (mainly 10-30 m depth, Kelly and Barker 1961 in Kenchington 1991), and is very common in the Gulf of Maine (Scott and Scott 1988). Here we concentrate on the first species, the deepwater redfish *S. mentella* (Figures 8 and 9). As its common name suggests, *S. mentella* is a deepwater, predominantly benthic species that rises off the bottom during the night (Scott and Scott 1988). However, mesopelagic groups have been documented in the Irminger Sea (Figure 8), and might represent separate stocks (Bel'skiy et al. 1987, Christensen and Pedersen 1989). Depth range of occurrence for *S. mentella* is 130-900 m (FishBase 1999), and stocks often show stratification by depth, with smaller individuals generally more shallow (Christensen and Pedersen 1989). Immature individuals have been recorded widely distributed down to 500 m (Drevetnyak 1993). However, no change in average length with depth was recorded for depths between 150-200 m, but average size did increase with depths > 200m (Magnusson et al. 1990). Redfish are ovoviviparous and larvae are born (extruded) at approximately 7 mm size after absorbing the eggsack. During the larval extrusion period adults were found to concentrate in the 250-700 m depth range (Drevetnyak 1993), with the majority of extrusions occurring at 250-400 m depth (Magnusson et al. 1990, Mukhina et al. 1992, 1995). The larval stage is pelagic in surface waters in 0-50 m depth (Christensen and Pedersen 1989, Herra 1989, Mukhina et al. 1992). Nursery areas are found mostly at depths between 50 and 350 m (Anon. 1998). At approximately 25 mm in size they start moving into deeper waters (Christensen and Pedersen 1989). Redfish grow to 7-8 cm during first year, thereafter approximately 2.5 cm per year until about 10 years of age, after which growth slows down (Scott and Scott 1988). Sexual maturity is thought to be reached at 8-10+ years of age, with a longevity of 40+ years (Christensen and Pedersen 1989).

DISCUSSION

The visualization of two-dimensional life history patterns, using the coastal transect method presented here, represents only a small component of the assessment of ecosystem effects of fishing undertaken by the *Sea Around Us Project*. Application of this method in the context of this project will require drawings of similar transects for the major commercial species of the North Atlantic, as defined by those species contributing 90% of the FAO database landings for FAO areas 21, 24 and parts of 31 and 34. This list will be augmented by species of regional significance based on 90% of the landings in the ICES and NAFO databases (e.g American lobster). It is anticipated that this might result in 40-50 species.

The purpose of these generalized life-history transects is not to present a detailed, quantitative depth distribution analysis. However, these graphics lend themselves to inclusion of such quantitative data in the form of vertical and horizontal data graphics that can be incorporated into the existing transects. Such quantitative information can be obtained from various sources, such as depth stratified survey data (e.g. Mahon and Sandeman 1985, Mahon et al. 1998).

Within the framework of the project, these coastal transect distributions will help assign catches to areas such as those described in the classification systems of the Large Marine Ecosystems (Sherman and Duda 1999) and 'biogeochemical provinces' (Longhurst 1995). A consensus synthesis approach to these classification systems is being considered by the *Sea Around Us Project* (see Pauly et al. 2000). The catch data allocation algorithm may also use augmentative data on geographic distribution and quantitative depth information where available (e.g. cumulative distribution frequency curves in Perry and Smith 1994). Within the context of the *Sea Around Us Project*, present day (1990s) as well as 'historic' transects (1950-60s) may need to be produced for stocks whose range of distribution may have changed significantly (e.g. Norwegian Spring Spawning herring present day versus 1970s, Figures 2 & 3). Additional information, such as seasonal variation in distribution or temperature iso-lines can also be accommodated, for example through multi-panel graphics. However, given the temporal and spatial scale of interest in this project (annual ecosystem models of large marine ecosystems) the present generalized 'snapshot' covering a distinct time period (e.g. 1990s) is considered appropriate.

Furthermore, Ruttan et al. (2000) will provide a method for assessing the yield and economic benefits gained and foregone through non-optimal use of resources by each fisheries sector (small scale versus large scale, incorporating gear type, vessel size and area of operation) for the different areas in the North Atlantic. The area and species specific information on the various scales of operation of different fishery sectors can thus be visually superimposed on the coastal transects, and coastal transects of fish distributions be used to show how different species 'connect', through their life history patterns, different fisheries sectors, such as small with large scale fisheries (e.g. inshore versus offshore).

Thus, we consider the present approach may be useful for visualizing the existence, interaction and potential conflicts between different fishery sectors for species or stocks whose life history patterns illustrate the need for improved integration of management of the different fishery sectors. This may apply in particular to rationalizations of overcapitalized fisheries. The proposed visualization may be used by management to incorporate the concept of life history interconnectivity between different fishery sectors and may assist in the formulation of more informed policy options for ecosystem-based management of North Atlantic fisheries.

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