Comparing Models of Trophic Flows in the Northern and Southern Benguela Upwelling Systems During the 1980s

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Abstract
Since 1981, the Benguela Ecology Programme has aimed at increasing ecological understanding of a large marine upwelling region of importance to fisheries. In an attempt to summarize results of this program, experts brought together both published and unpublished data at a workshop held in Cape Town in 1989. This was in an attempt to construct simple input-output carbon budgets of the Northern and Southern Benguela ecosystems. Based on these results, and together with more recently published data, ECOPATH models of the two systems during the 1980s have been prepared. In the Northern Benguela system, the dominant pelagic fish species during the 1980s was horse mackerel, whereas in the Southern Benguela, anchovy were dominant. In both systems, sardine were at low levels and hake were commercially important. These, together with different structures in the zooplankton communities and the different fishing levels in the respective systems, are used as a basis upon which to compare the trophic functioning of the two parts of the Benguela ecosystem during the period 1980-1989. Preliminary EcoSim analysis highlights differences in the impact of fisheries on selected groups in the two systems.
Introduction
There are four major marine upwelling systems in the world (Fig. 1). The Benguela upwelling system is subdivided into relatively distinct upwelling systems: the Northern Benguela off Namibia, and the Southern Benguela off South Africa. The trophic functioning of the Northern Benguela system has been examined in two periods, namely 1971-1977 and 1978-1983 (Jarre-Teichmann et al. 1998; Jarre-Teichmann and Christensen 1998a, 1998b). In addition, an ECOPATH model of the Northern Benguela has also been developed for the 1990s (Heymans 1996). Preliminary models of trophic flows in both the Northern (Shannon and Jarre-Teichmann 1999) and Southern (Jarre-Teichmann et al. 1998) Benguela systems during the 1980s have been constructed. The present paper serves as a preliminary comparison of the trophic functioning of the upwelling ecosystems of the Northern and Southern Benguela during this decade. The paper aims to stimulate and encourage further revision of the data and models, so that more detailed interdecadal and intersystem comparisons can be made. It is planned that this work will form part of a fuller comparison of the trophic functioning of both the Northern and Southern Benguela ecosystems during periods dominated by different species. Using an approach such as this, it would be possible to compare the way in which harvest and conservation strategies impact the northern and southern systems under different species dominance regimes. This would be of benefit to both South Africa and Namibia, particularly as the fisheries have been managed in different ways in the two systems over the last few decades. Researchers and managers in each system could learn from the other, and both could work together towards improving fisheries management and conservation in the future.

Methods
Trophic flow budgets for the Northern and Southern Benguela ecosystems during the 1980s were constructed using ECOPATH. The latter is a widely used ecosystem modeling tool that has been under development since 1987 by the International Centre for Living Aquatic Resources Management (ICLARM). Christensen and Pauly (1992, 1995) describe the ECOPATH model in detail. ECOPATH is based on a model by J.J. Polovina of the U.S. National Marine Fisheries Service, Honolulu, Hawaii (Polovina 1984). The steady state approach was recently extended to a dynamic simulation tool called ECOSIM by scientists of the Fisheries Centre, University of British Columbia, Canada (Walters et al. 1997).

At a workshop held in 1989, experts on the different species groups in the Benguela upwelling region brought together both published and unpublished data to construct a simple input-output carbon budget. These data, together with those which have since become available, have been used to construct preliminary Ecopath models of both the Southern (Jarre-
Teichmann et al. 1998) and the Northern (Shannon and Jarre-Teichmann 1999) Benguela upwelling systems. The model of the Northern Benguela comprises the shelf region to about 500 m depth, extends from 15ºS to 29ºS and covers an area of 179,000 km². The model of the Southern Benguela comprises the shelf region to about 500 m depth, extends from 29ºS, around the southern tip of Africa and eastwards to 28ºE, covering an area of 220,000 km². The Southern Benguela model, presented by Jarre-Teichmann et al. (1998), has been slightly modified to separate some components for clarity, and to incorporate some new hake data, which only recently became available. Parameters used are tabulated in Shannon et al. (1999). The two systems are compared in terms of flow diagrams, primary system statistics, relative consumption by components, primary production equivalents, and so on. In addition, analyses such as mixed trophic impact assessment (Ulanowicz and Puccia 1990) are used to highlight overall competition between species and the effects of species on others within an ecosystem.

ECOSIM has only been released in an alpha form at this stage. We show here how it can be used to perform preliminary analyses of the impacts of changing fishing mortality in the two systems. All settings were default, with interactions assumed to be of the mixed control type (0.5). Once thorough testing and validating of ECOSIM have been done, this work will be taken further.
Results and Discussion

Northern Benguela Model

In the Northern Benguela, there was heavy fishing on both sardine (*Sardinops sagax*) and hake (*Merluccius capensis* and *M. paradoxus*) during the 1970s. Sardine, the dominant pelagic species between 1971 and 1977 (Jarre-Teichmann and Christensen 1998a), was severely reduced from 1.5 million t to 134,000 t in the 1980s. Anchovy (*Engraulis capensis*) was also less abundant, decreasing from 593,000 t in the 1970s to 252,000 t in the 1980s. The dominant pelagic species was horse mackerel (*Trachurus trachurus capensis*), at 2.5 million t (Shannon and Jarre-Teichmann 1999). Biomass of hake (both species combined) was 1.3 million t in the 1980s. In order to balance the model, it was necessary to estimate the biomass of some groups, so that there was sufficient to support the consumption of other predatory groups. For example, the model required that biomass of demersal fish was half that of hake, an estimate that seemed reasonable (Shannon and Jarre-Teichmann 1999). Hewitson and Cruickank’s (1993) estimate of biomass of pelagic goby (*Sufflogobius bibarbatus*) was doubled in the model. The proportion of cephalopods in the diets of many species was reduced to avoid consumption of cephalopods exceeding production. Estimates of benthic fauna and production are lacking. Therefore the model was used to estimate required benthic biomass. That the benthic biota in the northern ecosystem are less abundant (at only 25% of that in the southern Benguela) is to be expected (Shannon and Jarre-Teichmann 1999); the northern model is of an upwelling area whereas the southern model extends over shelf (Agulhas Bank) and upwelling areas. Further, low oxygen levels are frequently found in shelf waters off Namibia (Bailey 1991).

Southern Benguela Model

During the 1980s, anchovy was the dominant pelagic fish, at a biomass of 1.1 million t off South Africa. Sardine was at a low level of only 129,000 t, mesopelagic fish (lanternfish, dominated by *Lampanyctodes hectoris* and lightfish, *Maurolicus muelleri*) at 1.7 million t, and hake at about 624,000 t (both species combined). In order that the model balance, some of the parameters of a few groups had to be reevaluated. Hake and other demersal fish caused major problems in the model, particularly related to diet composition of the various size groups. The proportion of these groups in the diet of others was reduced in many cases and it was necessary to allow the model to estimate the predatory biomass of these groups, based on the amount required as prey and catches. Hake biomass was required to be about 64% higher than estimated, and that of other demersal fish, 7.5 times higher. These adjustments can send ripple effects through the system as a result of prey species being consumed in larger amounts. As in the Northern Benguela, cephalopods were not abundant enough to support demands by other components, and the proportion in the diets of some groups had to be reduced dramatically.
Comparison of Northern and Southern Benguela Upwelling Systems

Summary Statistics
Total biomass (excluding detritus) was higher in the Northern Benguela (360 t per km²) than in the Southern Benguela (297 t per km²). With the exception of total catches, all major flows were higher in the Southern Benguela (Table 1), indicating that the Southern Benguela is a more productive system. Mean path lengths (sensu Finn 1976) in the two systems were similarly short, at 3.02 in the Southern and 3.19 in the Northern Benguela.

Flow Diagrams
Trophic levels of the components of the systems, biomasses, and flows through the two systems are compared (Fig. 2). Many components in the Southern Benguela occupy higher trophic levels than the same groups in the Northern Benguela.

Consumption
Consumption by anchovy, redeye, hake, and other demersal fish and mesopelagic fish are most important in the Southern Benguela (Fig. 3b). In the Northern Benguela (Fig. 3a), horse mackerel and goby also consume large portions of production.

Primary Production Required
Use of primary production equivalents enables the effects of fishing at different trophic levels to be compared (Pauly and Christensen 1995). The

Table 1. Comparison of summary statistics in the Northern and Southern Benguela upwelling systems in the 1980s. Flows are in tons per km² per year.

<table>
<thead>
<tr>
<th></th>
<th>Northern Benguela</th>
<th>Southern Benguela</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sum of all consumption</td>
<td>11,743</td>
<td>14,196</td>
</tr>
<tr>
<td>Sum of all exports</td>
<td>1,254</td>
<td>4,300</td>
</tr>
<tr>
<td>Sum of all flows to detritus</td>
<td>4,265</td>
<td>10,170</td>
</tr>
<tr>
<td>Total system throughput</td>
<td>23,327</td>
<td>36,435</td>
</tr>
<tr>
<td>Sum of all production</td>
<td>10,034</td>
<td>15,427</td>
</tr>
<tr>
<td>Net system production</td>
<td>1,254</td>
<td>4,300</td>
</tr>
<tr>
<td>Sum of all respiratory flows</td>
<td>6,065</td>
<td>7,769</td>
</tr>
<tr>
<td>Total net primary production</td>
<td>7,319</td>
<td>12,068</td>
</tr>
<tr>
<td>Total catches</td>
<td>7</td>
<td>3</td>
</tr>
</tbody>
</table>
Figure 2. Diagrams of the trophic flows in the Northern (top) and Southern (bottom) Benguela during the 1980s. Boxes arranged along vertical axis by trophic level. Flows are tons wet mass per km² per year. Biomass of components denoted by B where B > 1 t per km². Flows leave boxes in upper half, enter in lower half. Values are indicated for respiration and flows to detritus, with those less than 5 t per km² per year (i.e., around 0.3-0.4 ppt of total consumption) omitted for clarity.
Figure 3. Production consumed by predators in the Northern (a) and Southern (b) Benguela during the 1980s.
greatest proportions of total primary production required to support catches in the Southern Benguela are those of anchovy, large pelagic fish, and hake (Fig. 4). Catches of horse mackerel and hake require far greater proportions of total primary production in the Northern Benguela system. Primary production required for fisheries is 5.8% in the Northern and 3.6% in the Southern Benguela. That the fraction of primary production required to sustain catches in the Southern Benguela is so small, could be explained by the mismatch of phyto- and zooplankton productivity and fish consumption, as suggested by Hutchings (L. Hutchings, pers. comm., Marine and Coastal Management, South Africa). This seems not to be the case in the Northern Benguela.

By contrast, the ratio of primary production required by the fisheries, to harvest, is 179 in the Southern Benguela, compared to only 96 in the Northern Benguela. This indicates that fishing in the Southern Benguela is ecologically more expensive than in the Northern Benguela, despite lower catches in the south. The mean trophic levels of catches are similar in the southern (4.7) and northern (4.6) systems.

Primary production required to sustain (i.e., support the consumption) of top predators (large pelagics, seals, sharks, seabirds, whales, and dolphins) in the Southern Benguela was 1,553 t, compared to 657 t in the Northern Benguela system. This indicates that top predators are far more important in the Southern Benguela system, as also reflected in the catches of species serving as their prey.

**Trophic Aggregation**

Biomass was concentrated in trophic level I in the Northern Benguela and trophic level II in the Southern Benguela (Table 2). Transfer efficiencies were comparable between the two systems at most levels, with the exception of transfer through level IV in the southern system being twice as efficient as that in the northern system. As expected for upwelling systems (Christensen and Pauly 1993), the transfer efficiency at these high trophic levels is low, as are those at the herbivore level. There are some long food chains in both systems, resulting in a total of nine discrete trophic levels.

**Mixed Trophic Impact Assessment**

Mixed trophic impact assessment is a technique measuring the relative impact of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia 1990). It assumes that trophic structure is constant; i.e., the technique cannot be used for predictive purposes, but should rather be used as sensitivity analysis. In the Southern Benguela, microzooplankton benefited mesozooplankton, anchovy, sardine, redeye (*Etrumeus whiteheadi*), and other small pelagic fish, such as saury (*Scomberesocidae*) and flying fish (*Exocoetidae*), by providing a food source for these groups and by serving as food for others upon which
Table 2. Trophic aggregation in the Benguela upwelling systems during the 1980s.

<table>
<thead>
<tr>
<th>Trophic level</th>
<th>Biomass (t per km²)</th>
<th>Transfer efficiency, % (all flows)</th>
<th>Total throughput (all flows)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Northern</td>
<td>Southern</td>
<td>Northern</td>
</tr>
<tr>
<td>I</td>
<td>206.87</td>
<td>89.60</td>
<td>11,584.02</td>
</tr>
<tr>
<td>II</td>
<td>86.91</td>
<td>147.78</td>
<td>9,670.81</td>
</tr>
<tr>
<td>III</td>
<td>48.83</td>
<td>40.77</td>
<td>10.6</td>
</tr>
<tr>
<td>IV</td>
<td>14.55</td>
<td>14.58</td>
<td>12.3</td>
</tr>
<tr>
<td>V</td>
<td>3.02</td>
<td>4.27</td>
<td>17.5</td>
</tr>
<tr>
<td>VI</td>
<td>0.22</td>
<td>0.46</td>
<td>9.2</td>
</tr>
<tr>
<td>VII</td>
<td>0.01</td>
<td>0.02</td>
<td>7.3</td>
</tr>
<tr>
<td>VIII</td>
<td>0.00</td>
<td>0.00</td>
<td>3.0</td>
</tr>
<tr>
<td>IX</td>
<td>0.00</td>
<td>0.00</td>
<td>2.9</td>
</tr>
<tr>
<td>X</td>
<td>0.00</td>
<td>0.00</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Figure 4. Percent of total primary production required to sustain catches in the Northern and Southern Benguela ecosystem during the 1980s.
these groups prey (Fig. 5). By contrast, in the northern system, microzooplankton competed with these groups (goby replaces redeye in the northern system) for phytoplankton food, thereby having a net negative impact on them. Mesozooplankton, through consuming phytoplankton, negatively affected pelagic goby in the Northern Benguela. However, mesozooplankton was an important prey item for its counterpart in the Southern Benguela, the redeye. Owing to its greater biomass in the south, anchovy had more pronounced impacts on other groups in the Southern Benguela. Similarly, horse mackerel, the dominant pelagic species in the Northern Benguela, had greater effects on its competitors in the north. Sardine showed small net effects in both systems. As expected from higher catches in the Northern Benguela, groups in this system were more severely affected by fishing.

**ECOSIM Analysis of the Effects of Altered Levels of Fishing Mortality**

Altered fishing mortality has different effects in the two systems (Fig. 6a-c). Increasing fishing mortality (F) on the three most abundant small pelagic fish in each system (namely anchovy and sardine in both systems, and redeye in the south and goby in the north) had less pronounced effects on other components in the Northern than in the Southern Benguela (Fig. 6a). Anchovy and sardine stocks in both systems crashed under this scenario of fishing. Further, in the Southern Benguela, there was a sharper decline in large pelagic fish when their prey of anchovy and sardine were severely fished. Redeye and goby catches were very low and therefore increasing these by a factor of four appears to have little effect. Despite such low fishing effort on redeye and goby in the southern and northern systems, respectively, the ecotrophic efficiencies of these two groups are very high (greater than 0.9), indicating that they are in high demand as food for other groups. Fishing at higher absolute levels would have major implications for the systems. In the Southern Benguela, chub mackerel and horse mackerel were favored by decreases in anchovy and sardine biomass, leaving more zooplankton available to their competitors (refer also to Fig. 5b).

When fishing mortality was increased fourfold as above, but only for the first 4 years of the simulation, sardine in the Northern Benguela began to recover, although only reaching about one-third of its original biomass by year 10 (Fig. 6b). Anchovy did not recover. In the Southern Benguela, both species recovered by year 10.

Increasing fishing mortality of hake fourfold in the first four years of simulation reduced hake biomass, thereby favoring some of the prey species of hake, such as mesopelagic fish and squid (Fig. 6c). However, in the Northern Benguela, other small pelagic fish (e.g., saury) were reduced and did not recover once fishing on hake was restored to its original level. In both systems, horse mackerel were negatively affected by increased fishing on hake, stabilizing at a lower level of abundance once fishing on hake...
Figure 5. Mixed trophic impacts of selected groups in the Northern and Southern Benguela during the 1980s. Bars extending above the line of zero impact for each species represent net positive impacts. Conversely, bars extending below the zero line represent net negative impacts.
Figure 6. Results of ECOSIM simulations. Biomass plotted as a proportion of original biomass. (a) Effects of a fourfold increase in fishing mortality (F) of anchovy, sardine, and redeye (Southern Benguela) or goby (Northern Benguela) over 10 years. (b) Effects of a fourfold increase in fishing mortality (F) of anchovy, sardine, and redeye (Southern Benguela) or goby (Northern Benguela) for the first 4 years, after which Fs are set back to original levels. (c) Effects of a fourfold increase in fishing mortality (F) of hake for the first 4 years, after which F is set back to original level.

1 = Sardine
2 = Anchovy
3 = Cephalopods
4 = Small pelagics
5 = Chub mackerel
6 = Horse mackerel
7 = Hake
8 = Mesopelagics
9 = Redeye
10 = Large pelagics
11 = Other demersals
12 = Goby
was restored to its original level. The effect was more severe in the Southern Benguela. This is explained by the greater net negative impact which mesopelagic fish had on horse mackerel, by competing with them for zooplankton food (Fig. 5b).

As horse mackerel were lightly fished in the Southern Benguela, increasing $F$ by a factor of 4, for example, had little effect. In the Northern Benguela, increasing $F$ on horse mackerel fourfold for 4 years reduced horse mackerel biomass dramatically, so that by year 10, biomass was only at half its original level. Horse mackerel had a negative effect on chub mackerel by competing with them for zooplankton prey (Fig. 5a). Therefore chub mackerel were favored by this scenario, leveling off at a biomass factor of 1.7 that at the start.

**Conclusions**

There are clearly differences in the functioning of the Northern and Southern Benguela systems, related to abundances of the various components, as well as to the level of harvesting on these. Catches were higher in the Northern Benguela, despite the higher overall production in the Southern Benguela. However, fishing was more ecologically expensive in the southern system. Top predators were more important components in the Southern Benguela, as indicated by twice the primary production required to support consumption by top predators in the south. Demersal fish biomass required to support consumption in the Southern Benguela was double that in the Northern Benguela. However, when hake biomass is taken into account, the overall demersal component was only slightly higher in the Southern Benguela, and is explained by the fact that the Southern Benguela system is a continuum from upwelling to shallow bank. Although only lightly fished in both systems, mesopelagic fish, redeye, and pelagic goby were required to sustain the production of other components within the systems, and their heavier exploitation should be considered with caution. Zooplankton was more abundant in the Northern Benguela, but not as efficiently transferred to higher trophic levels.

Preliminary ECOSIM analyses show that increasing fishing mortality (in proportion to its original value) has different effects in the two systems, and that these are complex responses to indirect and direct competition. In the Southern Benguela, large pelagic fish were more severely affected by fishing strategies that reduce their small pelagic prey. Also, horse mackerel and hake were more closely linked, so that reducing hake biomass had a more pronounced effect on horse mackerel in the Southern Benguela.
Acknowledgments

We would like to thank Coleen Moloney, Patti Wickens and John Field for their foresight in organizing the workshop held in 1989, for which much of the basic data used in this model were prepared and presented by local experts. We thank Coleen Moloney for her encouragement and support in this first comparative attempt. We are grateful to the European Union Framework Programme IV, Cooperation with Third Countries and International Organisations, Part C, Scientific and Technological Cooperation with the Developing Countries “Putting fishing effects in the ecosystem context” for funding which enabled us to work together on this project. We thank Villy Christensen for his efforts to make available to us the alpha version of EcoSim used in this paper. Intentions to model this system for the period 1980-1989 were presented at the International Symposium on Environmental Variability in the South-east Atlantic, held 30 March-1 April 1998 in Swakopmund, Namibia, and parts of the manuscript presented were incorporated into this paper.

References


Modeling of Chub Mackerel (Scomber japonicus) and Sardine (Sardinops sagax melanosticta) During the Annual Migration Cycle

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Abstract
In this work we have attempted to mathematically describe chub mackerel (Scomber japonicus) and sardine (Sardinops sagax melanosticta) migrations, and construct a model and verify it by retrospective forecast. Three models are described. The first is constructed based on a linear migration model excluding any environmental factors. The second is constructed by taking into account the thermocline depth. The third model adds the additional characteristic of a temperature gradient in the thermocline. Positive results permit predicting migrations one month in advance for April-June and September-October for chub mackerel and for January-April and September-October for sardine.
Introduction

Fish of the genus *Scomber* are one of the most numerous fishes found in the pelagic waters of temperate and subtropical zones of the Pacific Ocean. Chub mackerel is widely distributed and occurs in the temperate waters around Japan, where it has periods of high abundance. Large aggregations of Pacific sardine are also observed in this area. The least understood aspects of the biology of these commercially targeted fish is their foraging and spawning migrations (Figs. 1 and 2). Therefore, forecasting these occurrences is very important for the fishing fleet.

The mathematical modeling of the spatial-temporal distribution of biological populations and communities is not well developed, as is the modeling of dynamics of their biomass (Bocharov 1990). Therefore the problem of modeling the migrations of pelagic fishes is quite practical.

Based on the scientific research of the distributions and migrations of chub mackerel and Pacific sardine, a problem arose in describing the seasonal migrations of these fishes by mathematical methods; i.e., constructing a model to obtain model coefficients and verify them with actual data.

We constructed three models based on a chamber model, where the considered biological population is divided into subpopulations (chambers), which are connected only by migration flows: i.e.,

\[
\frac{du_{ik}}{dt} = f_{ik}(u_{ik},...,u_{nk}) + M_{ik}(u_{i1},...,u_{in})
\]

where
- \( u_{ik} \) is biomass (abundance) of species \( i \) in fragment \( k \);
- \( f_{ik} \) is intrapopulation interaction of species \( i \) in fragment \( k \);
- \( M_{ik} \) is inflow of migrants of species \( i \) in fragment \( k \); and
- \( n \) is number of species.

The main advantage of the chamber approach is the simplicity of the model. Considering the use of ordinary differential equations, chamber
Figure 1. Distribution of chub mackerel in the northwest Pacific (Belayev 1984).
1 = Spawning region, 2 = Foraging region, 3 = Migrations, 4 = Month.

models carry out the analysis rather easily, which was one of the factors for selecting them for the mathematical description of migrations of the studied biological objects.

In considering the construction of the migration models, we divide the ocean surface into equal squares and attach each square to a coordinate grid \([i, j]\). Use data on catch per effort (in kilograms) as density of fish concentration in each square in the given month and designate it as \(X_{ij}\). By considering one of the squares in the given month \((n)\) we take four adjacent squares on the horizontal and vertical, and assume at the current time the fish migrate from square to square; i.e., movement between squares (subpopulations) occurs.
Figure 2. Scheme of northern migrations of Pacific sardine (Kenya 1982). 1 = Oyashio branches, 2 = Direction of moving sardine assemblage, 3 = Warm waters, 4 = Cold waters, 5 = Sardine aggregations.
For the simplicity in model appearance, we designate fish concentrations in the adjacent squares as $X_1, X_2, X_3,$ and $X_4$.

**Model 1**

We designate a coefficient $a$ in our model, and obtain a linear forecast equation for the following month ($n+1$) for the given square $X_{ij}^*$:

$$X_{ij}^*(n+1) = X_{ij}(n)(1 - 4a) + X_1(n)a + X_2(n)a + X_3(n)a + X_4(n)a.$$

Group items with respect to the coefficient $a$:

$$X_{ij}^*(n+1) = X_{ij}(n) + aX_1(n) + X_2(n) + X_3(n) + X_4(n) - 4X_{ij}(n).$$

For simplicity, let:

$$c = X_1(n) + X_2(n) + X_3(n) + X_4(n) - 4X_{ij}(n),$$

then the predicted fish concentration for month $n+1$ for the given square is:

$$X_{ij}^*(n+1) = X_{ij}(n) + ac.$$

Write the residual sums of squares:

$$U = \sum_n \left[ X_{ij}^*(n+1) - \bar{X}_{ij} \right]^2,$$

where $\bar{X}_{ij}$ are observed data, then minimize the obtained function:

$$U \rightarrow \text{min}.$$

Equating the partial derivative with respect to parameter $a$ to zero, we obtain equation:
\[ \frac{\partial U}{\partial a} = 2 \sum_n (X_{ij}^*(n+1) - \bar{X}_{ij})c = 0. \]

After some transformations we obtain the solution, i.e., coefficient of the model:

\[ a = \frac{\sum_n c[\bar{X}_{ij} - X_{ij}(n)]}{\sum_n c^2}. \]

**Model II**

Through extensive statistical analyses, scientists have revealed that oceanographic factors, such as the depth of a thermocline and its gradients of temperatures (Sokolovskiy 1971), greatly influenced the distribution of chub mackerel in waters of 11-16°C.

Therefore in our model we limit fish migrations to depth of the thermocline; i.e., assume that fish will migrate in the direction where the thermocline is deeper. Given the differences of thermocline depth between one square and its adjacent squares \( r_1, r_2, r_3, \) and \( r_4, \) and designating coefficients \( a \) and \( b, \) we obtain a linear forecast equation for the following month \( (n+1) \) for the given square \( X_{ij}^* \):

\[
X_{ij}^*(n+1) = X_{ij}(n)[1 - 4a - 4b(\rho_1 + \rho_2 + \rho_3 + \rho_4)] + X_{ij}(n)(a + b\rho_1) + X_{ij}(n)(a + b\rho_2) + X_{ij}(n)(a + b\rho_3) + X_{ij}(n)(a + b\rho_4).
\]

Group items with respect to coefficients \( a \) and \( b: \)

\[
X_{ij}^*(n+1) = X_{ij}(n) + a[X_1(n) + X_2(n) + X_3(n) + X_4(n) - 4X_{ij}(n)] + b[X_1(n)\rho_1 + X_2(n)\rho_2 + X_3(n)\rho_3 + X_4(n)\rho_4 - 4X_{ij}(n)(\rho_1 + \rho_2 + \rho_3 + \rho_4)].
\]

Let:

\[
c = X_1(n) + X_2(n) + X_3(n) + X_4(n) - 4X_{ij}(n),
\]

\[
d = X_1(n)\rho_1 + X_2(n)\rho_2 + X_3(n)\rho_3 + X_4(n)\rho_4 - 4X_{ij}(n)(\rho_1 + \rho_2 + \rho_3 + \rho_4),
\]

the predicted fish concentration for month \( n \)

\[
X_{ij}^*(n+1) = X_{ij}(n) + ac + bd.
\]

Write the residual sums of squares:
\[
U = \sum_n [X^*_i(n+1) - \bar{X}_{ij}]^2.
\]

Then minimize the obtained function:

\[
U \rightarrow \text{min}.
\]

Equating the partial derivative with respect to parameters \(a\) and \(b\) to zero, we get a closed system of two equations with two unknown parameters:

\[
\begin{align*}
\frac{\partial U}{\partial a} &= 2\sum_n (X^*_i(n+1) - \bar{X})c = 0, \\
\frac{\partial U}{\partial b} &= 2\sum_n (X^*_i(n+1) - \bar{X})d = 0
\end{align*}
\]

Having made some transformations, we obtain the solutions to our system, i.e., coefficients of the model, where \(a\) is expressed as an implicit form:

\[
b = \frac{\sum_n c^2 \sum_n d(\bar{X}_{ij} - X_{ij}(n)) - \sum_n c d \sum_n c(\bar{X}_{ij} - X_{ij}(n))}{\sum_n c^2 \sum_n d^2 - (\sum_n c d)^2},
\]

\[
a = \frac{\sum_n c(\bar{X}_{ij} - X_{ij}(n)) - b \sum_n c d}{\sum_n c^2}.
\]

**Model III**

To have a model more flexible in response to hydrological conditions, we add one more coefficient \(c\) with regard to gradient in the thermocline. Assigning \(g_1, g_2, g_3\), and \(g_4\) as the differences of gradients in the thermocline between one square and its adjacent squares, we obtain a linear forecast equation for the following month \((n+1)\) for the given square \(X^*_i\):

\[
X^*_i(n+1) = X_{ij}(n)[1 - 4a - 4b(\rho_1 + \rho_2 + \rho_3 + \rho_4) \\
- 4c(g_1 + g_2 + g_3 + g_4)] + X_i(n)(a + b\rho_1 + cg_1) \\
+ X_2(n)(a + b\rho_2 + cg_2) + X_3(n)(a + b\rho_3 + cg_3) \\
+ X_4(n)(a + b\rho_4 + cg_4)
\]

Group items with respect to coefficients \(a, b\) and \(c\):
\[ X^*_n(n+1) = X^*_0(n) + a[X^*_1(n) + X^*_2(n) + X^*_3(n) + X^*_4(n)] - 4X^*_ij(n) + b[X^*_1(n)\rho_1 + X^*_2(n)\rho_2 + X^*_3(n)\rho_3 + X^*_4(n)\rho_4] - 4X^*_ij(n)(\rho_1 + \rho_2 + \rho_3 + \rho_4) + c[X^*_1(n)g_1 + X^*_2(n)g_2 + X^*_3(n)g_3 + X^*_4(n)g_4] - 4X^*_ij(n)(g_1 + g_2 + g_3 + g_4) \]

Again let:

\[ l = X^*_1(n) + X^*_2(n) + X^*_3(n) + X^*_4(n) - 4X^*_ij(n), \]

\[ m = X^*_1(n)\rho_1 + X^*_2(n)\rho_2 + X^*_3(n)\rho_3 + X^*_4(n)\rho_4 - 4X^*_ij(n)(\rho_1 + \rho_2 + \rho_3 + \rho_4), \]

\[ n = X^*_1(n)g_1 + X^*_2(n)g_2 + X^*_3(n)g_3 + X^*_4(n)g_4 - 4X^*_ij(n)(g_1 + g_2 + g_3 + g_4). \]

The predicted fish concentration for month \( n+1 \) for the given square is:

\[ X^*_n(n+1) = X^*_0(n) + al + bm + cn. \]

Minimize the residual sums of squares:

\[ U = \sum_n [X^*_n(n+1) - \overline{X}_j]^2. \]

Equating the partial derivative with respect to parameters \( a, b, \) and \( c \) to zero, we obtain a closed system of three equations with three unknowns:

\[
\begin{align*}
\frac{\partial U}{\partial a} &= 2\sum_n \left[X^*_n(n+1) - \overline{X}\right]l = 0, \\
\frac{\partial U}{\partial b} &= 2\sum_n \left[X^*_n(n+1) - \overline{X}\right]m = 0, \\
\frac{\partial U}{\partial c} &= 2\sum_n \left[X^*_n(n+1) - \overline{X}\right]n = 0
\end{align*}
\]

Make replacement:

\[ X = \overline{X}_j - X^*_0(n). \]

Put the system into matrix:
Solve the system using the Gauss method. For this purpose let:

\[
\begin{align*}
R_1 &= \left( -\frac{\sum l^2}{\sum lm} \right), \\
R_2 &= \left( -\frac{\sum l^2}{\sum ln} \right), \\
R_3 &= \left( -\frac{\sum lm + R_1 \sum m^2}{\sum lm + R_2 \sum mn} \right), \\
R_4 &= \sum ln + R_3 \sum mn + R_3 \left( \sum ln + R_2 \sum n^2 \right), \\
R_5 &= \sum lx + R_4 \sum mX + R_3 \left( \sum lx + R_2 \sum nX \right)
\end{align*}
\]

then:

\[
\begin{align*}
a\sum l^2 + b\sum lm + c\sum ln &= \sum lx, \\
b \left( \sum lm + R_1 \sum m^2 \right) + c \left( \sum ln + R_1 \sum mn \right) &= \sum lx + R_1 \sum mX, \\
c(R_4) &= R_5
\end{align*}
\]
After some transformations, we obtain the implicit solutions to our system, i.e., coefficients of the model:

\[
\begin{align*}
    c &= \frac{R_5}{R_4}, \\
    b &= \frac{\sum_{n} (\sum_{n} mX - c(\sum_{n} \ln + R_1 \sum_{n} mn))}{\sum_{n} \sum_{n} m^2}, \\
    a &= \frac{\sum_{n} (\sum_{n} X - b \sum_{n} \ln - c \sum_{n} \ln)}{\sum_{n} I^2},
\end{align*}
\]

**Data**

As the basis of our work we used materials collected in TINRO surveys in 1984-1986, including chub mackerel catch per unit of effort data (kg per hour) and water temperature in a 0-600 m layer at 34°15′-44°30′N and 141°-160°E. Data on chub mackerel and sardine catches (SDD [ship daily data] from work of the Soviet-Russian fishing fleet) from 1980 to 1992 were used. A file of long-term, deepwater data, created by the employees of DVNIGMI was also used, where the temperature data were arranged on 1 degree squares in each month of a year for a layer of 0-500 m. Data processing for the above three sources is as follows.

**Survey Data**

Survey data for 1984-86 were interpolated in units of a regular square grid with steps of 15 minutes (0.25°) with the help of the graphic package Surfer (Win32) (Version 6.01, Surface Mapping System, Copyright 1993-95, Golden Software Inc.). (Survey data were not averaged.) Various methods of interpolation of data in this software are widely available. For interpolation of our data we used the method of "Inverse Distance to a Power." This gridding method is a weighted average interpolator, and can be either an exact or a smoothing interpolator. The power parameter controls how the weighting coefficients drop off as distance from a grid node increases. For a larger power, closer data points are given a higher fraction of the overall weight; for a smaller power, the weights are more evenly distributed among the data points.

The weight given to a particular data point when calculating a grid node is proportional to the inverse of the distance to the specified power of the observation from the grid node. When calculating a grid node, the assigned weights are fractions, and the sum of all the weights is equal to 1.0.
When an observation is coincident with a grid node, the observation is given a weight of essentially 1.0, and all other observations are given a weight of almost 0.0. In other words, the grid node is assigned the value of the coincident observation. This is an exact interpolator. Graphic representation of data on chub mackerel is shown in Fig. 3a and 3b. For an example of interpolated data for chub mackerel in September see Table 1a-c.

As the duration of the survey was lengthy, coefficients of migrations for some months were not obtained for the models.

**Commercial Data**

Commercial data for 1980-1992 were averaged for the fishing period by months. For this purpose the data array was divided by months, and the region of fishing for each month was broken into a regular square grid node in 3-minute segments (0.05°). Data in each square were averaged for the center of the square. An example of a long-term data array on sardine fishing is shown in Fig. 4.

These data were then also interpolated in nodes of a regular grid by steps of 6 minutes (0.1°) by the same method of interpolation in the Surfer32 software. An example of interpolated data for sardine in October is in Table 2a-c.

**Hydrological Data**

Hydrological data provided from the files of DVNIGMI were averaged and interpolated in nodes of a regular grid with steps of 6 minutes (0.1°) by the same method of interpolation in the Surfer32 software.

A program was written in the language of a high level Turbo Pascal (Version 7.0, Copyright 1983-92, Borland International, Inc.) to compare data from two nearest months, calculate coefficients of the models, and make prediction using the obtained coefficients.

**Conclusions**

For chub mackerel on scientific surveys we obtained coefficients for models II and III, some of which are indicated below:

September-October:

\[ a = 0.3987151, b = 0.0235035; \]
\[ a = 0.3851383, b = 0.0334592, c = 0.00280627; \]

April-May:

\[ a = 0.4358854, b = 0.0051921; \]
\[ a = -0.8897466, b = 0.0028711, c = 0.08901928; \]

May-June:

\[ a = 0.0579618, b = 0.0027537; \]
\[ a = 0.0888050, b = 0.0010291, c = 0.03524888. \]
Coefficients were also obtained using three models on monthly distribution data averaged over many years for sardine fishing, some of which are indicated below:

January-February:
\[ a = 0.3220480; \]
\[ a = 0.2684861, b = 0.0017835; \]
\[ a = 0.2743469, b = 0.0033472, c = 0.0740538; \]

February-March:
\[ a = 0.4763302; \]
\[ a = 0.3867460, b = 0.0020080; \]
\[ a = 0.3579247, b = 0.0001139, c = 0.0670430; \]

March-April:
\[ a = 0.3945235; \]
\[ a = 0.3208751, b = 0.0007745; \]
\[ a = 0.3131046, b = 0.0001545, c = 0.0727093; \]

September-October:
\[ a = 0.2780193; \]
\[ a = 0.2337730, b = 0.0479562; \]
\[ a = 0.2171924, b = 0.0264501, c = 0.0014328. \]

Based on the work we have done, we conclude:

1. Models of chamber type give rather reliable results pertaining to the actual data; i.e., the retrospective forecast errors are insignificant, taking into account the quantity of information used.

2. Data arrays on chub mackerel and sardine fishing, obtained from scientific surveys and during fishing, as well as hydrological data are well interpolated using the Surfer32 graphic package.

3. Figures 5-9 drawn with the help of the Surfer32 graphic package show that predicted fish concentrations are smoother than the actual data, but the general trend in the distribution of biological objects is maintained.

4. Based on the coefficients of migrations obtained from the survey data on chub mackerel, it is seen that the beginning of spawning (southern) migrations is rather heavily influenced by the change of thermocline depth, and the beginning of foraging (northern) migrations by vertical temperature gradients.

5. The same conclusions can be made on coefficients of migrations, obtained through the application of long-term fishing data on sardine.
Figure 3a. Graphic representation of data on chub mackerel for September. Top = catch per effort (kg per hour), Middle = the depth of thermocline (m), and Bottom = temperature gradient (°C per m) in the thermocline for September.
Figure 3b. Graphic representation of data on chub mackerel for September. Top = catch per effort (kg per hour), Middle = the depth of thermocline (m), and Bottom = temperature gradient (°C per m) in the thermocline for September.
Table 1a. Data on catch per effort (kg per hour).

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<tr>
<th>Latitude</th>
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<th>42.75°N</th>
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Table 1b. Data on depth of thermocline (m).

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Table 1c. Data on a gradient in thermocline (ºC/m).

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Figure 4. Data array from daily ship data from the Soviet-Russian fleet fishing for sardine 1980-1992.
Table 2a. Data on catch per effort (kg per hour).

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Table 2b. Data on depth of thermocline (m).

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Table 2c. Data on a gradient in thermocline (°C per m).

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Figure 5a. Distribution of chub mackerel in May. Top = actual data forecasted from April, Middle = Model II, Bottom = Model III.
Figure 5b. Distribution of chub mackerel in May. Top = actual data forecasted from April, Middle = Model II, Bottom = Model III.
Figure 6a. Distribution of sardine in April. Top = actual data forecasted from March, Middle = Model II, Bottom = Model III.
Figure 6b. Distribution of sardine in April. Top = actual data forecasted from March, Middle = Model II, Bottom = Model III.
Figure 7a. Distribution of sardine in May. Top = actual data forecasted from April, Bottom = Model III.
Figure 7b. Distribution of sardine in May. Top = actual data forecasted from April, Bottom = Model III.
Figure 8. Distribution of sardine in May. Top = actual data forecasted from April, Bottom = Model III.
Figure 9a. Distribution of sardine in May. Right = actual data forecasted from April, Left = Model III.
Figure 9b. Distribution of sardine in May. Right = actual data forecasted from April, Left = Model III.
6. In view of the above it is possible to conclude that the assumptions stated by the Sokolovskiy (1971) and Belayev (1984) that chub mackerel and sardine distribution is dependent on the depth of the thermocline, and the temperature gradient in the thermocline are confirmed.

References


