OBSERVER EFFECTS ON PELAGIC FLEET OPERATIONS AND BAYESIAN-BASED EXPLORATIONS OF THE MASS BALANCE MODEL ECOPATH

By

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DECLARATION

This thesis reports the results of original research, carried out in the Department of Mathematics and Applied Mathematics (University of Cape Town) in consultation with Marine and Coastal Management. This work has not been submitted in whole or in part for a degree at any other University. All of the data that are presented were obtained from sources that have been fully acknowledged and assistance that I have received has also been fully acknowledged.

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ABSTRACT

This thesis comprises two sections. The first deals with the analysis of observer data from pelagic commercial vessels with a particular focus being to examine whether there is any indication of dumping (discarding) that is provided by these data. The second section investigates the ability of constraints associated with the ECOPATH mass-balance equations to improve knowledge on estimates of parameters in the southern Benguela ecosystem.

Sardine and anchovy are the most valued and carefully managed species of small pelagic fish in South Africa. The problem of dumping in this pelagic fishery has been recognised for some time. The reasons for dumping are thought to arise, *inter alia*, from large bycatches of sardine (counting against a bycatch allowance) with anchovy and unsuitable sizes of sardine caught for canning purposes. As there were no data that could be used as a basis to investigate the claims, little was done to substantiate them. The Observer Programme to collect data from commercial vessels was instituted in 1999. These data are analyzed to establish whether there are any appreciable differences in catch rates between vessels with observers and those without. General Linear Models (GLMs) are used to adjust for the effects of other factors that could confound comparisons because of the non-random nature of observer placement.

Central to the analyses of these data are different catch rate measures. The first measure used is catch per time at sea, which is referred to as CPUETS: the catch of the species concerned made by a vessel on a trip divided by the total number of hours it takes for the vessel to steam from port to the fishing ground, fish and then return to the port. The second measure is catch per haul, which is referred to as CPUEH. This measure divides catch by the total number of hauls made by the vessel during that trip. The CPUETS was the preferred measure due to concerns related to the CPUEH measure (essentially greater reliability of the data and less potential for bias being introduced through other effects which influence haul size). Catch rates were modelled with errors assumed to follow either a log normal or a Poisson distribution. The Poisson error model was the preferred model based on features of the standardized residuals.

The results obtained indicate higher catch rates when observers are on board pelagic vessels. Based on the results from the Poisson error model, the magnitude of the observer effect (and hence possible dumping) could be some 60% for sardine catches made between January and June, and some 20% for anchovy catches between May and October. However these results must be considered as preliminary as Marine and Coastal Management is rechecking the validity of the data used in a process that will allow account to be taken of some additional possible co-variates in the GLM standardisation.

The use of the ECOPATH with ECOSIM software around the world when analysing ecosystem data has been on the increase during the past decade. Given the "black box" nature of this software, it is important to scrutinise its mathematical fundamentals and the underlying methodology. In this study an investigation is conducted as to whether ecotrophic and food conversion constraints associated with the set of linear equations that comprise ECOPATH are capable of improving knowledge about estimates of biomass and productivity available from other sources such as surveys.

Uncertainties were added to point estimates of biomass and production to biomass ratios. Markov Chain Monte Carlo (MCMC) was used to integrate over these uncertainties in a way that takes account of the constraints introduced by ECOPATH. In summary:

1. There is a general decrease in uncertainty for both biomasses *(B)* and production:biomass *(P/B)* ratios in percentage terms. The level of improvement increases with increases in the extent of uncertainty input. In other words, when the space of the input priors is large enough, the ECOPATH constraints do lead to posterior distributions which reflect non-trivial improvements in uncertainty. However, if input uncertainties are low, the ECOPATH constraints do not provide much by way of updating/improvement.
2. Inspection of different improvements achieved if some inputs were known with greater certainty indicates that improved precision of inputs for *P/B* would be more valuable than improvements for diet composition.

Further work should ideally repeat these analyses using specific estimates of uncertainty for parameters for each species/species group considered, rather than the species- independent constants used for the illustrative analyses presented here.

OVERVIEW OF THESIS

This thesis comprises two sections. Section A deals with the application of General Linear Models (GLMs) to investigate the impact observers have on catch rates for the South African pelagic fleet. The focus is on anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*). The details of the contents of each Chapter in Section A are explained in this section's introduction. Section B deals with Markov Chain Monte Carlo (MCMC) to investigate the potential of constraints associated with ECOPATH (Christensen *at al.* 2004) to improve biomass ***(B)*** and production:biomass ***(P/B)*** estimates of selected species groups.

Outline of Section B

Chapter 9 introduces ECOPATH, discusses a potential problem and provides a conceptual overview of how the problem might be solved.

Chapter 10 introduces the mathematical basis of ECOPATH and the constraints associated with it.

Chapter 11 explains the previous work that has been carried out in the Southern Benguela region and the available data for the study.

Chapter 12 explains the MCMC methods followed for the analyses and the illustrative application of the methodology to the Southern Benguela data.

Chapter 13 explains a general method followed in analyzing the data from the MCMC algorithms and presentation of some results.

Chapter 14 discusses the results with respect to different scenarios explored.

Chapter 15 gives the concluding remarks and future work.

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SECTION A:

DO OBSERVERS ON BOARD PELAGIC FISHING VESSELS AFFECT CATCH RATES?

CHAPTER 1

INTRODUCTION

There are six species targeted by purse-seiners in South African waters. These are sardine (*Sardinops sagax)*, also known as pilchard in South Africa, anchovy (*Engraulis encrasicolus)*, horse mackerel (*Trachurus trachurus capensis*), chub mackerel (*Scomber japonicus*), roundherring (*Etrumeus whiteheadi*) and lantern fish (*Lampanyctodes hectoris*) (de Oliveira, 1995) which are sustained by the highly productive waters of the Benguela current upwelling region. Details of the distribution and life history of sardine and anchovy are summarised in Fig. 1.1. The pelagic fishery is South Africa's second most valuable in monetary terms, and provides the highest yields in terms of landed mass. It is also the most dynamic fishery, because the species which it targets are relatively short-lived, often occur in mixed shoals and experience large fluctuations in abundance (de Oliveira, 2003). Sardine and anchovy are by far the most important of the species targeted by the South African pelagic fishery in terms of the landed value. Hence in this study the focus is on these two species only.

The dynamics of the fisheries pose a number of operational challenges to those who harvest the resource, such as pressures to fill their quotas before the fishing season ends and difficulties in targeting a particular species when species can occur in mixed shoals. These challenges usually lead to undesirable behaviour such as discarding (dumping) of fish. In the South African pelagic fishery an observer programme was started in 1999 to collect the data on board the commercial vessels for various research objectives. The nature of the data collected is explained under section 2.3 (Data from observers) in Chapter 2. The data that were collected are used in this study to investigate the impact the presence of observers may have on the fishing behaviour of vessels, with a particular focus being to examine whether there is any indication of dumping that is provided by these data, and whether the associated extent can be quantified.

This is the first study to investigate the impact that the presence of observers has on fishing behaviour in the pelagic fishery since the inception of the observer programme in 1999. The study seeks to establish whether there is any evidence which suggests that the catch rates of vessels with an observer on board are appreciably different from the catch rates of vessels without observers. It is already clear from observer reports that some vessels do discard fish even if observers are on board vessels (see Chapter 3). If such malpractice is greater in the absence of observers, one would expect such vessels to show lower catch rates because they discard more than vessels with observers.

Fishing activities worldwide have generally progressed from a primarily food gathering activity to a means of generating income, so that discarding is based on economic considerations. Factors that may influence discarding may be related to markets, hold capacity, and regulations. The decision as to which part of the catch to dump is driven mainly by these factors (Chen *et al.* 1996). A study by Science and Technology Options Assessment (STOA), a European Parliament division on policy options, classifies motivation for discards into economic reasons and actions induced by some management measures. STAO lists the following economic motivations for dumping (www.onefish.org):

a) "Target species may be discarded because they are below minimum landing size, or damaged upon capture so as a result will not be acceptable to the market.
b) Target species which are acceptable to the market and legal to land may still be discarded in favour of better size or quality, an activity which is generally termed high grading.
c) Marketable non-target species which have a lower value than the target species may be dumped to preserve storage capacity required for higher priced target species.
d) Non-target species may be dumped if there is no monetary return to be derived once landed".

Thus discards may consist of marketable species (e.g. over-quota or lower value catches) or of non-marketable fish (e.g. juveniles or species with no market value). STAO also cites discarding induced by management measures such as minimum landing size (MLS); other factors related to quota arrangements have not been fully researched.

Since the inception of the observer programme in the South African pelagic fishery, observers have estimated the amount of fish that was discarded as well as citing reasons for discarding, as reported in Chapter 3. Specific situations thought to perhaps lead to discarding in the South African pelagic fishery include:

a) Large bycatches of juvenile sardine with anchovy because of concerns that this is not suitable for (high value) canning, or will count against bycatch limits and hence may lead to curtailment of anchovy fishing before a rights holder reaches their anchovy quota.

b) Sardines are not of the right size for optimal canning yield.

c) Species caught are not that immediately required by a factory given processing limitations.

d) Anchovy catch would take up storage capacity probably reserved for higher valued sardine.

The insights gained from this study constitute a stepping stone towards improving monitoring and further quantification of the amount of fish discarded in the pelagic fishery. Although the effect of dumping has in the past been implicitly included in the mortality parameter when pelagic resource assessments are carried out, some progress at least in quantifying this factor will assist in the quantification of yield forgone, and provide a starting point towards addressing the problem.

Chapter 2 of the study details all the data sources considered and how these were combined to form one data base for analyses, while excluding those data points considered unreliable following a validation exercise. Chapter 3 provides the preliminary analysis of the data with emphasis on the formulation and investigation of catch rates stratified by the observer factor. In Chapter 4 preliminary analyses from Chapter 3 are extended using statistical methods. Chapter 5 reports analyses similar to those of Chapter

4, but carried out for a smaller set of data. Chapters 6 and 7 consider model diagnostics and provide the final conclusions of the study. Chapter 8 suggests areas that need further investigation.

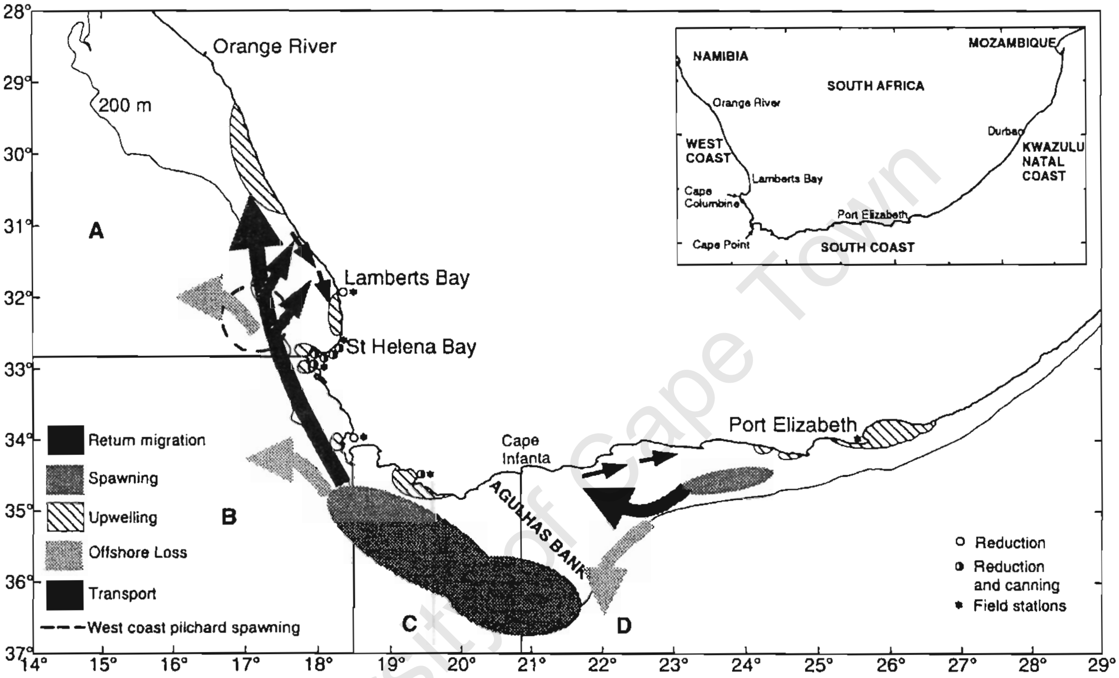

Figure 1.1: Conceptual map of the distribution and movement of sardine and anchovy (from Coetzee 2001).

CHAPTER 2

SOURCES OF DATA

The amalgamated data used in this study spans a period of almost 6 years (covering January 1999 to August 2004), and amounts to in excess of 60 thousand records. The data came from four different sources: inspectors, the skippers of the vessels, observers that are placed on these vessels and a vessel data file kept by Marine and Coastal Management (MCM) that lists the characteristics of each vessel.

2.1. Data from inspectors

The operating procedure for all vessels in the pelagic fishery is that when landings are made, they are declared to a fishery inspector at the harbour. This inspector classifies catches into dominant species, juvenile and adult fish, and determines the actual catch made by the vessel. The information about the trip that is recorded by inspector is listed in Table 2.1.

Table 2.1: The descriptions of the fields on an inspector's data form, together with the units of measurement for some fields.

Field	Description	Units
a) Departure date	The date and time (nearest minute) at which the vessel leaves port	-
b) Arrival date	The date and time (nearest minute) at which the vessel arrives back at port	-
c) Vessel code	The identification code given to each vessel, which is the same as that given on the observer's and skipper's data form	-
d) Targeted species	The dominant species in the catch by the vessel	-
e) Catch	This refers to the tonnage made for each species; the tonnage could either be for targeted catch or for bycatch	tonnes
f) Catch category	An indication of whether the catch is directed or bycatch	-
g) Fish Size	The fish size category gives an indication whether a fish is an adult or a juvenile	-
h) Factory code	A code assigned to the factory to which the vessel belongs or for which it is landing	-

2.2. Data from skippers

The skippers also record data about the catches made during the period at sea. Table 2.2 lists these data. Note that for certain of these data (those related to individual hauls), the skipper's form is the only source of this information.

Table 2.2: Descriptions of the fields on the skipper's data form together with the unit of measurement for some fields.

Field	Description	Units
a) Arrival date	The date and time (nearest minute) at which the vessel arrives back to port	-
b) Vessel code	The identification code given to each vessel, which is the same as that given on the observer's and the inspector's data forms	-
c) Haul date	The date and time (nearest minute) at which hauls were made	-
d) Haul position	The position (this is a square of 10x10 nautical miles) of each haul made	-
e) Catch	An estimates of the catch made for each haul, stratified by species type	tonnes
f) Species	The dominant species for each haul on a trip	-

2.3. Data from observers

The data that have been consistently collected over the period from 1999 to August 2004 by the observers are listed in Table 2.3. Haul duration and pumping rates were recorded for the year 2000 only.

Table 2.3: Description of the fields on an observer's data form together with the units of measurement for some fields. Note that discarded catch is not always stratified by species.

Field	Description	Units
a) Departure date	The date on which the vessel leaves port	-
b) Arrival date	The date on which the vessel arrives back at port	-
c) Sail port	The port from which the vessel leaves	-
d) Land port	The port to which the vessel returns to offload	-
e) Vessel code	The identification code given to each vessel, which is the same as that given on inspector's and skipper's data forms	-
f) Species	The main species targeted	-
g) Position	The position (square of 10x10 nautical miles) of each haul that is made	-
h) Discards	The amount of catch discarded during the trip	tonnes
i) Other vessels	The names of other vessels fishing in the same vicinity	-
j) Reasons	The reasons for each case when discarding occurs	-

k) Length frequency	The length frequency for samples from some hauls for dominant species	-
l) Haul duration	The duration of each haul	minutes
m) Pump rate	The pumping rate of fish for each haul	tonne/min

2.4. Vessel Data

All the characteristics of vessels operating in South African waters are recorded and kept by MCM. Table 2.4 list the details recorded for the vessels in pelagic fisheries. In most cases some information about a vessel is absent. Table 2.5 provides the proportion of pelagic fishing vessels for which information is available for each characteristic.

Table: 2.4 Vessel characteristics that are recorded in the MCM vessel database. The Table also provides a description of each vessel characteristic, and the units where applicable.

Characteristic	Description	Units
a) Vessel code	The identification code given to each vessel, which is the same as that given on the inspector's, the observer's and the skipper's data forms	-
b) Vessel name	The name given to a vessel	-
c) Vessel length	The length of the vessel	metres
d) Vessel group	Vessels are grouped as bait, ordinary or steel vessels	-
e) Factory	The name of the factory to which the vessel belongs	-
f) Port	The name of the port at which the vessel is registered	-
g) Freezer	An indication of whether or not a vessel has a freezer	-
h) Crew	The number of people that are usually on the vessel	-
i) Registration	Details the country of registration,	-
j) Propulsion	An indicator of the power of the vessel	kilowatts

Table 2.5: The proportion of pelagic fishing vessels for which various characteristics are recorded. Note the proportion listed by the Table indicates the proportion of vessels for which various characteristic are recorded (for example, the freezer characteristic was only recorded for 10% of the vessels, not meaning that only 10% of vessels have freezers).

CHARACTERISTIC	PROPORTION WITH INFORMATION (%)
Vessel code	100
Vessel name	100
Vessel length	97
Vessel group	94
Factory	44
Port	44
Freezer	10
Crew number	61
Registration	92
Propulsion	60

2.5. Combined data

The data that are the most completely recorded are those by the fishery inspectors when vessels return from the fishing trip to port. Thus these data were chosen as the base to which all the other sources of data (from skippers, observers and information about vessels) were linked for analyses. Accordingly most of the data selected for use for these analyses were taken from those recorded by inspectors. However, some fields that related to hauls were available only in the other data bases, and therefore these data were extracted from those data sources. The unique fields for linking the data sources were the arrival and departure dates together with the vessel codes, which are the same for each source. The fields for the resultant file of combined data are listed in Table 2.6; Microsoft Office Access 2003 was used to link the data.

Table 2.6: Combined data from the four data sources: inspector, skipper, observer and vessel characteristics.

Field	Source of data	Units
a) Departure date	Inspector's data form	-
b) Arrival date	Inspector's data form	-
c) Vessel code	Inspector's data form	-
d) Targeted species	Inspector's data form	-
e) Catch	Inspector's data form	tonnes
f) Catch category	Inspector's data form	-
g) Fish Size	Inspector's data form	-
h) Factory code	Inspector's data form	-
i) Port	Vessel's data form	-
j) Vessel length	Vessel's data form	metres
k) Vessel type	Vessel's data form	-
l) Trip length	Evaluated from Inspector's arrival and departure dates	hours
m) Month	Taken to be reflected by arrival date	-
n) Year	Ranges from 1999 to 2004	-
o) Total number of hauls	Skipper's data form	-
p) Observer presence	Provided the dates and vessels codes from inspector and observer forms match.	-

2.6. Identification of potential errors in the combined data base

In a data set as large as the pelagic fishery data base, typographical errors are bound to occur. It is almost impossible to detect all erroneous data points for particular variables in this large a dataset; the ones that are easier to detect are those at the extremes. Identifying and removing the data points found at the extreme ends of distributions, which may hence be unduly influential, has its potential problems. For example, the data point removed could be a genuine observation from a heavy-tailed distribution which has large and important influence when other factors are estimated when fitting a model (Glazer, 1999). There are a number of methods for identifying outliers in the literature (these include plotting of residuals against predicted values and explanatory variables, Principal components and Basic Structure Display). In this study the General Linear Models (GLMs) were fitted first, and then observations associated with hauls and hours were removed on the basis that they reflected large residual values (see Besley *et al.* 1991).

When standardised residuals were plotted against the explanatory variables (hauls and hours), points lying outside the convex hull evident for the (hauls, hours)-space were investigated further. These were points associated with hours greater than 300 and hauls greater than 14 for both species (sardine and anchovy). For sardine only 12 data points (these include values associated with hours and hauls) were removed, amounting to only 3 in 10 000 of data discarded, and for anchovy 11 data points were removed amounting to only 4 in 100 000 discarded. All these data points discarded were also regarded as unrealistic by MCM.

CHAPTER 3

PRELIMINARY ANALYSIS OF PELAGIC FISHERY AND OBSERVER DATA

3.1. The placement of observers on vessels

The vessels in the pelagic fishery are classified into three broad groups. The first is the bait vessel: these are smaller vessels which are generally less then 20 metres long. The second group is so-called ordinary vessel: these are middle sized vessels mainly between 20 and 26 metres long. The third is steel vessels: these are larger vessels which are generally greater than 27 metres long.

The placement of observers was not random among these vessels. At the beginning of the program, observers were preferentially placed on mid-sized and bigger vessels (i.e. the second and third groups) for reasons of operational convenience. This placement was gradually spread to smaller vessels catching sardine starting in 2001 (see Table 3.1). (Note: In the Tables and the text that follow, separation between sardine and anchovy is on the basis of the dominant species in the catch. Bycatch is included only if this is mentioned specifically). Observers have not yet been placed on bait vessels fishing for anchovy.

Table 3.1: Proportional placement of observers on vessels by vessel group, stratified by year and for trips where either sardine or anchovy was the dominant species caught.

	Sardine			***Anchovy***		
	bait	ordinary	steel	bait	ordinary	*steel*
	Percentage coverage			***Percentage coverage***		
Year						
1999	0	64%	36%	0	74%	*26%*
2000	0	62%	38%	0	71%	*29%*
2001	6%	42%	52%	0	73%	*27%*
2002	4%	94%	2%	0	93%	*7%*
2003	16%	48%	13%	0	61%	*39%*
2004	*31%*	*56%*	*13%*	*0*	*74%*	*26%*

3.2. The observer coverage

The average proportion of trips with observer coverage over the period of the study was about 3.5% percent for sardine and somewhat higher for anchovy at about 6% (see Table 3.2).

Table 3.2: Total number of trips made from January 1999 to August 2004 stratified by observer presence for sardine and for anchovy as the dominant species caught. Percentage coverage indicates proportion of trips that had observers.

	Sardine			***Anchovy***		
	Absence or presence of observers			*Absence or presence of observers*		
Year	Trips without	Trips with	% coverage	Trips without	Trips with	*% coverage*
1999	4541	42	1%	2297	78	*3%*
2000	4264	13	0.3%	2858	103	*3%*
2001	5637	428	8%	3876	464	*11%*
2002	6293	53	0.2%	2743	28	*1%*
2003	15935	727	5%	8494	632	*7%*
2004	5021	185	1%	2359	130	*5%*
Total	***41691***	***1448***	***3.5%***	***22627***	***1435***	***6.3%***

3.3. Comparisons of catches with and without observers

There are numerous ways in which catch rates could be calculated, with some being more meaningful than others in the context of this study. For the purpose of preliminary analysis, three ways of measuring catch rates were explored. The first measure was catch per time at sea, which is referred to as CPUETS: the catch of the species concerned made by the vessel on a trip divided by the total number of hours it takes for a vessel to steam from port to the fishing ground, fish and then return to the port. The second measure is the catch per haul, which is referred to as CPUEH. This is a measure where catch is divided by the total number of hauls made by the vessel during that trip.

The last measure is the catch per trip (CPUETR) which is the total catch made by the vessel over a time period divided by the total number of trips it made during that period.

These catch rates were stratified by observer presence over the period of the study to see what effect such presence had on catch rates (see Tables 3.3, 3.4 and 3.5). The figures given in these Tables are not definitive because they have yet to be adjusted to make allowance for the non-random nature of observer placement (this will be addressed in the next chapter). It is of note that for sardine where there is poorer observer coverage, catch rates in terms of CPUETS and CPUEH are higher for those cases when observers are present though this is not the case for anchovy. However, when the data are stratified by vessel group (bait, ordinary and steel) category (Tables 3.4 and 3.5.), the catch rates per trip (CPUETR) are generally higher for anchovy when observers are on board the vessels, but there is no clear pattern for sardine.

Table 3.3: Catch rates for both sardine and anchovy in relation to observer presence.

a) CPUETS - catch (in tonnes) per hour at sea

	CPUETS			
	Sardine		***Anchovy***	
	Observer		*Observer*	
Year	Absent	Present	Absent	*Present*
1999	1.63	0.50	4.05	*6.13*
2000	1.71	1.15	5.58	*7.56*
2001	2.15	2.60	4.55	*5.64*
2002	2.67	1.33	4.76	*2.94*
2003	2.58	2.30	4.10	*6.86*
2004	2.26	2.54	3.79	*5.17*
Total	***2.17***	***1.74***	***4.47***	***5.72***

b) CPUEH - catch (in tonnes) per haul

	CPUEH			
	Sardine		***Anchovy***	
	Observer		*Observer*	
Year	Absent	Present	Absent	*Present*
1999	14.48	2.84	26.72	*31.74*
2000	17.14	10.50	35.67	*47.60*
2001	19.78	19.54	29.55	*28.12*
2002	23.33	9.55	33.09	*21.88*
2003	19.86	13.60	28.78	*35.98*
2004	20.94	12.23	25.26	*25.54*
Total	***19.26***	***11.38***	***29.84***	***31.81***

Table 3.4: Analysis of sardine catches stratified by year, vessel group and observer presence (observer presence is indicated by yes, absence by no) in terms of catch per trip (CPUETR).

Sardine								
			Trips		Catch(tonnes)		*Catch (tonnes) per trip*	
Year	Vessel group	No of vessels	no	yes	no	yes	no	*yes*
1999	Bait	26	1133		13369.63		11.80	
	Ordinary	55	2554	27	58092.60	174.02	22.75	*6.45*
	Steel	13	854	15	60218.21	201.31	70.51	*13.42*
2000	Bait	28	1320		17898.28		13.56	
	Ordinary	50	2043	8	43101.85	89.77	21.10	*11.22*
	Steel	15	889	5	73217.80	120.40	82.36	*24.08*
2001	Bait	27	1847		27908.77		15.11	
	Ordinary	48	2435	174	48365.62	4799.05	19.86	*27.58*
	Steel	16	1237	240	103928.57	17499.23	84.02	*72.91*
2002	Bait	21	2161	2	35412.73	27.13	16.39	*13.57*
	Ordinary	51	2490	51	77471.24	1223.57	31.11	*23.99*
	Steel	16	1259		128991.55		102.46	
2003	Bait	21	2531	41	46214.04	831.94	18.26	*20.28*
	Ordinary	48	3051	125	84686.78	2181.74	27.76	*17.45*
	Steel	16	1197	97	112535.87	5431.62	94.01	*56.00*
2004	Bait	21	1678	54	30125.97	1074.57	17.95	*19.90*
	Ordinary	44	2037	96	56236.80	1648.93	27.61	*17.18*
	Steel	16	818	32	87321.28	2043.42	106.75	*63.86*
	Total		***31534***	***967***	***1105099***	***37346.7***	***35.04***	***38.62***

Table 3.5: Analysis of anchovy catches stratified by year, vessel group and observer presence (observer presence is indicated by yes, absence by no) in terms of catch per trip (CPUETR).

Anchovy								
			Trips		Catch(tonnes)		*Catch per trip (tonnes)*	
Year	Vessel group	No of vessels	no	yes	no	yes	no	*yes*
1999	Bait	1	1		0.1		0.1	
	Ordinary	52	2010	58	137848.04	4847.15	68.58	*83.57*
	Steel	12	286	20	34894.63	3181.96	122.01	*159.10*
2000	Bait	3	32		248.70		7.77	
	Ordinary	49	2388	73	194472.34	5913.68	81.44	*81.01*
	Steel	13	438	30	59786.14	5319.68	136.50	*177.32*
2001	Bait	1	2		14.76		7.38	
	Ordinary	45	3119	329	217304.29	29222.49	69.67	*88.82*
	Steel	15	627	124	50665.02	11096.89	80.81	*89.49*
2002	Bait	1	1		0.41		0.41	
	Ordinary	47	2025	26	141010.80	1277.35	69.64	*49.13*
	Steel	16	557	2	61322.01	57.36	110.09	*28.68*
2003	Bait							
	Ordinary	42	5807	61	151565.96	12341.50	26.10	*202.32*
	Steel	16	1891	245	62586.90	10333.14	33.10	*42.18*
2004	Bait	2	3		18.23		6.08	
	Ordinary	39	1674	93	93298.12	116.2	55.73	*1.25*
	Steel	16	499	33	45855.11	2660.36	91.83	*80.62*
	Total		**21360**	**1094**	**1250891**	**86367.74**	**58.56**	***78.95***

3.4. Identification of the causes for dumping

Observers record the estimated tonnage of fish discarded when dumping occurs, as well as the reasons why it occurred in some instances. A basic analysis of these data was conducted to get some sense of the extent of dumping as indicated by observers, as well as the reasons recorded for such discarding. The tonnage specified is not always stratified by species, so the values in Tables 3.6 and 3.7 are for sardine and anchovy together.

Table 3.6: Number of trips each year for which dumping is reported in vessels with observers. An estimate (in tonnes) of the amount discarded is not always made in all these instances, as reflected in the Table. Total trips and tonnage are not stratified by species. The estimated total annual tonnage of discarded fish as recorded by the observers is given in the last column.

year	Trips with estimates of dumping	Trips with no estimates of dumping	Total trips with dumping recorded	Total trips with observers	Percentage trips with observers where dumping reported	*Annual estimated tonnage dumped*
1999	2	3	5	120	2%	*3*
2000	2	2	4	116	3%	*56.5*
2001	21	2	23	892	3%	*220.26*
2002	16	3	19	580	3%	*551.69*
2003	11	3	14	1359	1%	*279.25*
2004	8	12	20	913	2%	*103*
Total	**60**	**25**	**85**	**3980**	**2%**	***1213.7***
percentage	***71%***	***29%***	***2%***			

Table 3.7: Reasons recorded by observers for dumping taking place during the periods of this study. The numbers of trips for which each particular reason was listed is shown, together with the corresponding proportion.

Reasons	Trip number	*Percentage*
Mechanical Faults	18	*21%*
Accidents	2	*2%*
Length Small	9	*11%*
Wrong species	7	*8%*
Boat full	27	*32%*
Not enough to warrant catching	5	*6%*
Reason not stated	*17*	*20%*

3.5. Preliminary conclusion

Considering the various simple measures of catch rate presented here, there are general indications that these rates are higher for anchovy with observers present than without, though the pattern for sardine is less clear. However, these results are not reliable as the placement of observers on vessels was not random. Thus further Chapters apply GLM methods to attempt to correct for the effects of other factors on these catch rates.

CHAPTER 4

THE USE OF GENERAL LINEAR MODELS (GLMS) TO QUANTIFY OBSERVER EFFECTS

4.1. Need for the use of GLMs

It is evident from Table 3.1 that the placement of observers on vessels has not been random across the vessel groups, particularly for sardine. Thus analyses have to take account of other factors which may influence catch rates, to avoid drawing incorrect conclusions about the effects associated with observers. General Linear Models (GLMs) are an accepted scientific method to do this, and are frequently used to "standardise" catch per unit effort (CPUE) indices for use in fitting population models (e.g. Glazer 1999). The aim of developing these GLM models is to see if the presence of an observer remains a statistically significant factor after all the other factors possibly influencing the catch rates have been taken into account. If the observer factor is significant, what is then of interest is the size and the sign of the effect; again the application of GLMs provides this information.

4.2. Proposed models and their error structures

Two measures of catch rates have been explored using GLMs: catch per hour at sea (CPUETS) and catch per haul (CPUEH) (see section 3.3) (Catch per trip (CPUETR) was not explored further as it is a coarser measure and so likely to reflect greater variance about underlying resource trends). These response variables are assumed to be related to explanatory variables for which data are available in a linear manner, as indicated by equations (4.1) and (4.2). The errors associated with these equations when relating them to the actual data are first assumed to be log-normally distributed, yielding equations (4.3) and (4.4).

$$CPUETS = \frac{catch}{hour} = \exp(\text{Linear combination of explanatory variables } + \varepsilon) \tag{4.1}$$

$$CPUEH = \frac{catch}{haul} = \exp(\text{Linear combination of explanatory variables } + \varepsilon) \tag{4.2}$$

$$\log_e(CPUETS) = \log_e(\frac{catch}{hour}) = \text{ Linear combination of explanatory variables} + \varepsilon \tag{4.3}$$

$$\log_e(CPUEH) = \log_e(\frac{catch}{haul}) = \text{Linear combination of explanatory variables} + \varepsilon \tag{4.4}$$

where:

ε is the error term assumed to be normally distributed with mean zero and constant variance σ^2.

These catch rates were also modelled using log-linear models where the errors were assumed to follow Poisson distributions, as indicated in equations (4.5) and (4.6).

$$Catch = Hours * \exp(\text{Linear contribution of explanatory variables}) + \varepsilon \tag{4.5}$$

$$Catch = Hauls * \exp(\text{Linear contribution of explanatory variables}) + \varepsilon \tag{4.6}$$

where:

ε is the error term assumed to be Poisson distributed.

Note that on log-transformation, equations 4.5 and 4.6 became linear in the explanatory variables, with $\log_e(Hours)$ and $\log_e(Hauls)$ then becoming offsets.

The explanatory variables considered are listed in Table 4.1.

Table 4.1: Descriptions of explanatory variables considered when modelling CPUETS or CPUEH. The symbol μ is used to denote the intercept in GLM equations. Note that all these variables are treated as discrete in the GLMs considered, except for hours and hauls which are treated as continuous if included, with associated parameters α and σ respectively.

Factor	Description	Units
$\kappa_{fishSize}$	Fish size with two levels: adults, juveniles	-
$\beta_{observer}$	Observer factor with two levels: either present or absent	-
$\gamma_{catchCategory}$	Catch category factor with two levels: either directed or by-catch	-
$Hours$	Total time taken for the trip	Hours
$Hauls$	Total number of hauls made during the trip	-
ϕ_{months}	Month factor with twelve levels: Jan… Dec	-
φ_{year}	Year factor with 6 levels: 1999 to 2004	-
$\eta_{vesselGroup}$	Vessel factor with three levels: bait, ordinary, steel	-
$\theta_{vesselLength}$	Vessel length with 24 levels	-
$\vartheta_{factory}$	Factory factor with ten levels	-

Note: Data for 2004 to August only as further data for that year were not yet available.

4.3. Factor selection for the models

A systematic way of selecting the factors to include in the final models was followed. First, a model consisting of a constant alone (the intercept μ) was evaluated. This was followed by adding the observer factor; a dummy variable showing the presence or the absence of an observer. Then all the other factors were added using the forward selection method as described by McCullagh and Nelder (1989). Thus, each factor was added one at a time and the deviance (-2 log likelihood) reduction calculated; at each iteration the factor that led to the greater reduction in deviance was retained, as long as this reduction was statistically significant (as determined by the 5 % χ^2 value for one degree of freedom). At the next step, with a selected factor included, each factor was added in turn and the process repeated. The observer factor was kept throughout as this was the factor of interest being investigated.

4.4. Application of GLMs

The GLMs[1] were first applied to the data before outliers were removed to provide a sound basis for such removals. Since the quantity of interest is the estimate associated with the presence of an observer, the presentation of results is usually restricted to the provision of the estimate of the associated parameter. Four models were explored on this basis. The model types considered are labelled as models 1 to 4 (for easy reference) below, and take into account all the factors for which data are available (though not interactions between these factors). However, the selected models as given in equations (4.7) to (4.10) show only selected factors.

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[1] The GLMs were conducted using GENSTAT version 7

The model type labelled ("model 1") shows the case when the effort is measured in total number of hours spent per trip (i.e. CPUETS) and the error distribution (after log transformation) is assumed to be normal. The second type "model 2" is the same as the model 1 except that the effort is measured in total number of hauls per trip (i.e. CPUEH). The third type "model 3" assumes a Poisson error model with effort in hours as an offset. The fourth model type is the same as the third except that effort is measured in hauls.

Model 1

$$\log_e(CPUETS) = \mu + \beta_{observer} + \alpha(Hauls) + \phi_{month} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \varepsilon \tag{4.7}$$

Model 2

$$\log_e(CPUEH) = \mu + \beta_{observer} + \sigma(Hours) + \phi_{month} + \kappa_{fishSize} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \varepsilon \tag{4.8}$$

Model 3

$$\log_e(catch) = \mu + \beta_{observer} + \log_e(Hours) + \phi_{month} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \varepsilon \tag{4.9}$$

where $\log_e(Hours)$ is an offset.

Model 4

$$\log_e(catch) = \mu + \beta_{observer} + \log_e(Hauls) + \phi_{month} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \varepsilon \tag{4.10}$$

where $\log_e(Hauls)$ is an offset.

The errors ε are normally distributed for models 1 and 2, and for models 3 and 4 reflect a Poisson distribution of the observed catch.

4.5. Preliminary results from GLMs

When the outliers were removed, GLMs were applied to the data using the models outlined above. The results of the models selected using the procedure outlined in section 4.3 are presented in Table 4.2. The parameter estimate reported is the size of the observer effect when the selected model is fitted.

Table 4.2: Estimates of the observer effect β (together with its standard error in parenthesis) for the selected model for each of the four types of model fitted. The standard error is given in brackets with the estimate itself in bold when the observer effect is statistically significant at 5% level.

species	model	Error model	Selected model	Observer effect and its std error
sardine	$\log_e\left(\frac{catch}{hours}\right)$			
		Log normal	$\alpha(Hauls)+\mu+\beta_{observer}+\gamma_{catchCategory}+\theta_{vesselLength}+\phi_{month}+\varphi_{year}+\varepsilon$	**0.22**(0.05)
	$\log_e\left(\frac{catch}{hauls}\right)$	Log normal		
			$\sigma(Hours)+\mu+\beta_{observer}+\gamma_{catchCategory}+\eta_{vesselGroup}+\phi_{month}+\varphi_{year}+\varepsilon$	0.03(0.05)
	$\log_e(catch)$	Poisson		
			$\log_e(Hours)+\mu+\beta_{observer}+\gamma_{catchCategory}+\phi_{month}+\eta_{vesselGroup}+\varphi_{year}+\varepsilon$	**0.19**(0.04)
	$\log_e(catch)$	Poisson		
			$\log_e(Hauls)+\mu+\beta_{observer}+\gamma_{catchCategory}+\phi_{month}+\eta_{vesselGroup}+\varphi_{year}+\varepsilon$	-0.03(0.04)
anchovy	$\log_e\left(\frac{catch}{hours}\right)$	Log normal		
			$\mu+\beta_{observer}+\gamma_{catchCategory}+\eta_{vesselGroup}+\alpha(Hauls)+\phi_{month}+\varphi_{year}+\varepsilon$	**0.10**(0.02)
	$\log_e\left(\frac{catch}{hauls}\right)$	Log normal		
			$\mu+\beta_{observer}+\gamma_{catchCategory}+\eta_{vesselGroup}+\sigma(Hours)+\phi_{month}+\varphi_{year}+\varepsilon$	0.02(0.02)
	$\log_e(catch)$	Poisson		
			$\log_e(Hours)+\mu+\beta_{observer}+\gamma_{catchCategory}+\eta_{vesselGroup}+\phi_{month}+\varphi_{year}+\varepsilon$	**0.19**(0.03)
	$\log_e(catch)$	Poisson		
			$\log_e(Hauls)+\mu+\beta_{observer}+\gamma_{catchCategory}+\eta_{vesselGroup}+\phi_{month}+\varphi_{year}+\varepsilon$	0.03(0.02)

Table 4.2 indicates that for both sardine and anchovy fishing, the presence of an observer has a positive effect on catch rates for log normal models when catch per hour at sea is used and for Poisson error models with log*(Hour)* as an offset. The sizes of effects are statistically significant at the 5% level. However, when the log normal models with catch per haul and the Poisson Model with log(Hauls) as an offset are used, the observer effect diminishes, with the size of the effect varying between -0.03 and 0.03 and not statistically significant at 5% level.

4.6. Further refinements of the models

So far only main effects have been considered when applying GLMs. These assume that the observer effect is the same whatever the year, month or type of vessel. To check whether the observer effect is in fact constant, interactions were introduced.

The effect of the observer on catch rates by month and year was investigated by incorporating the interaction terms between the observer factor and month, and between the observer factor and year into equations (4.7) to (4.10) to yield equations (4.11) to (4.14). The observer factor was redefined to reflect the effect of an observer in each of the two seasons of the year yielding equations (4.15) to (4.18). Other interactions that were investigated included those between the observer factor and catch category, hauls and hours. All the interactions except for the month interaction were found to be unimportant so that the associated results are not included in this study. Interaction between the observer factor and vessel group factor are not considered here, but rather in the next Chapter.

$$\log_e(CPUETS) = \mu + \beta_{observer} + \gamma_{catchCategory} + \eta_{vesselGroup} + \varphi_{year} + \phi_{month} + \alpha(Hauls) + \zeta_{observer \times year} + \xi_{observer \times month} + \varepsilon \qquad (4.11)$$

$$\log_e(CPUEH) = \mu + \beta_{observer} + \gamma_{catchCategory} + \eta_{vesselGroup} + \varphi_{year} + \phi_{month} + \sigma(Hours) + \zeta_{observer \times year} + \xi_{observer \times month} + \varepsilon \qquad (4.12)$$

$$\log_e(catch) = \log_e(Hours) + \mu + \beta_{observer} + \phi_{month} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \zeta_{observer \times year} + \xi_{observer \times month} + \varepsilon \qquad (4.13)$$

$$\log_e(catch) = \log_e(Hauls) + \mu + \beta_{observer} + \phi_{month} + \varphi_{year} + \eta_{vesselGroup} + \gamma_{catchCategory} + \zeta_{observer \times year} + \xi_{observer \times month} + \varepsilon \qquad (4.14)$$

$$\log_e(CPUETS) = \mu + \beta_{Observer'} + \varphi_{year} + \phi_{month} + \gamma_{catchCategory} + \eta_{vesselGroup} + \alpha(Hauls) + \varepsilon \qquad (4.15)$$

$$\log_e(CPUEH) = \mu + \beta_{Observer'} + \varphi_{year} + \phi_{month} + \gamma_{catchCategory} + \eta_{vesselGroup} + \sigma(Hours) + \varepsilon \qquad (4.16)$$

$$\log_e(catch) = \log_e(Hours) + \mu + \beta_{Observer'} + \varphi_{year} + \phi_{month} + \gamma_{catchCategory} + \eta_{vesselGroup} + \varepsilon \qquad (4.17)$$

$$\log_e(catch) = \log_e(Hauls) + \mu + \beta_{Observer'} + \varphi_{year} + \phi_{month} + \gamma_{catchCategory} + \eta_{vesselGroup} + \varepsilon \qquad (4.18)$$

where:

$\beta_{Observer'}$ is the observer factor with three levels indicating the presence of observer in each of the two seasons and the absence of an observer.

4.7. Results

Tables 4.3 and 4.4 give results for these refined models for catch rates in terms of hours and hauls respectively. They first show results of the analyses without interactions. The interactions between the observer and month factors were inspected to discover how the observer effect varies over a twelve month period, and this gave a clear indication of the patterns. On the basis of the pattern indicated by the interactions, the observer factor was aggregated to reflect the effect of the observer presence from January to June and from July to December for sardine, and from May to October and from November to April for anchovy (see Table 4.3). A similar process was followed to produce results in Table 4.4 – see equations (4.15) to (4.18).

The results presented in Table 4.3 clearly show higher catch rates in the presence of observers for the period May to October for anchovy, and even higher catch rates for the period January to June for sardine, than over the rest of the year. Table 4.4 gives results that are somewhat similar to those of Table 4.3, but smaller in size and for some months results have opposite signs to those in Table 4.3.

Measuring catch rates using hours at sea seems to be the preferable method as it gives clearer results than does catch per haul (Table 4.3 compared to Table 4.4). Hours at sea might also be a more reliable measure for two major seasons than catch per haul because other operational considerations might influence haul sizes and the information comes from sources other than the skippers alone. The next Chapter thus concentrates on $\log_e(CPUETS)$ as in equations (4.11) and $\log_e(catch)$ as in equation (4.13), when considering steel and ordinary vessels separately.

Table 4.3: Consolidated results for the $\log_e(CPUETS)$ model (with (log-) normal errors) and the $\log_e(catch)$ model (with Poisson errors) side by side. For each type of species there are three scenarios: the first is when only the main factors were fitted into the model; the second is when the observer effect differs for each month (i.e. an interaction between the observer factor and month); the last scenario is when the month factor is aggregated to show the effect of an observer between January to June and July to December for sardine, and between May to October and November to April for anchovy. The values in parentheses are standard errors.

Sardine			
		logCPUETS	Logcatch
	Month	Observer	Observer
No interactions		**0.22** (0.05)	**0.19** (0.04)
Interaction	Jan	0.51 (0.52)	-0.01(0.19)
	Feb	**0.81** (0.26)	**0.77**(0.12)
	Mar	0.23 (0.18)	**0.46**(0.12)
	Apr	**0.89** (0.20)	**0.44**(0.16)
	May	**0.60** (0.14)	**0.47**(0.12)
	Jun	0.20 (0.12)	**0.42**(0.17)
	Jul	**-0.60** (0.17)	-0.27(0.21)
	Aug	-0.33 (0.20)	0.26(0.19)
	Sep	**0.24** (0.11)	-0.16(0.10)
	Oct	0.21 (0.14)	0.07(0.08)
	Nov	0.04 (0.21)	0.01(0.09)
	Dec	0.30 (0.33)	0.14(0.12)
Aggregation	Jan-Jun	**0.45**(0.07)	**0.50**(0.06)
	July-Dec	0.01(0.07)	0.02(0.04)
Anchovy			
		logCPUETS	Logcatch
	Month	Observer	Observer
No interactions		**0.10** (0.02)	**0.19**(0.03)
Interaction	Jan	**-0.61**(0.29)	-2.11(3.88)
	Feb	**0.54**(0.25)	0.19(1.77)
	Mar	0.05(0.16)	-0.92(0.69)
	Apr	-0.07(0.08)	-0.06(0.14)
	May	**0.20**(0.06)	**0.41**(0.10)
	Jun	0.04(0.05)	**0.18**(0.07)
	Jul	**0.16**(0.06)	**0.39**(0.08)
	Aug	**0.22**(0.06)	**0.44**(0.07)
	Sep	0.04(0.03)	0.06(0.04)
	Oct	0.10(0.06)	**0.15**(0.08)
	Nov	0.32(0.22)	-0.83(1.60)
	Dec	0.04(0.03)	0.06(0.04)
Aggregation	May-Oct	**0.10**(0.02)	**0.20**(0.03)
	Nov-Apr	-0.01(0.06)	-0.13(0.14)

Table 4.4: Consolidated results for the $\log_e(CPUEH)$ model (with (log-) normal errors) and $\log_e(catch)$ model (with Poisson errors) side by side. For each type of species there are three scenarios: the first is when only the main factors were fitted into the model; the second is when the observer effect differs for each month (i.e. an interaction between the observer factor and month); the last scenario is when the month factor is aggregated to show effect of an observer between January to June and July to December for sardine, and between May to October and November to April for anchovy. The values in parentheses are standard errors.

Sardine			
		logCPUEH)	Logcatch
	Month	Observer	Observer
No interactions		0.03(0.05)	-0.03(0.03)
Interaction	Jan	0.42(0.46)	-0.01(0.17)
	Feb	0.22(0.24)	0.20(0.11)
	Mar	0.10(0.17)	**0.23**(0.11)
	Apr	**0.51**(0.18)	**0.30**(0.14)
	May	0.15(0.13)	**-0.21**(0.10)
	Jun	-0.05(0.11)	-0.07(0.10)
	Jul	**-0.78**(0.16)	**-0.50**(0.18)
	Aug	**-0.43**(0.18)	0.26(0.17)
	Sep	**0.29**(0.10)	-0.04(0.09)
	Oct	0.04(0.13)	-0.07(0.07)
	Nov	-0.19(0.19)	**-0.18**(0.07)
	Dec	0.31(0.30)	0.13(0.11)
Aggregation	Jan-Jun	**0.23**(0.08)	0.06(0.05)
	July-Dec	-0.07(0.06)	-0.07(0.04)
Anchovy			
		logCPUEH)	Logcatch
	Month	Observer	Observer
No interactions		0.02(0.02)	0.03(0.02)
Interaction	Jan	**-0.61**(0.25)	-1.95(3.22)
	Feb	0.22(0.21)	-0.20(1.43)
	Mar	-0.08(0.13)	-0.95(0.55)
	Apr	**-0.20**(0.07)	**-0.26**(0.11)
	May	0.06(0.05)	0.06(0.08)
	Jun	-0.03(0.04)	0.01(0.06)
	Jul	0.05(0.05)	0.08(0.06)
	Aug	**0.13**(0.05)	**0.21**(0.06)
	Sep	0.04(0.03)	0.04(0.04)
	Oct	-0.04(0.04)	-0.10(0.06)
	Nov	0.32(0.19)	-0.68(1.29)
	Dec	0.04(0.03)	0.04(0.04)
Aggregation	May-Sep	0.03(0.02)	**0.05**(0.02)
	Oct-Apr	**-0.13**(0.05)	**-0.31**(0.01)

CHAPTER 5

CONSIDERATION OF DIFFERENT VESSEL GROUPS

5.1. Data for ordinary and steel vessels

Steel vessels account for 40 % of the trips and 51 % of the total catch of sardine made by pelagic fishery vessels. They also account for 21 % of the trips and 26% of the catches of anchovy. The numbers of steel and ordinary vessels varies from year to year: for steel vessels there were between 13 and 16 and for ordinary vessels between 44 and 55 over the period of the study (see Table 3.5). Ordinary vessels account for 46 % of the trips and 33 % of the total catches made for sardine. They account for 79 % of the trips and 74% of the catches of anchovy. Investigating the effect of the observers on catch rates of these two groups of vessels separately was considered a desirable exercise to see if there were any differences in pattern. There were insufficient bait vessels with data to include them as a separate category.

5.2. GLM application to ordinary and steel vessels

Equations (4.7) and (4.9) were modified to include the actual vessels that made the catches. Vessel names were used to differentiate vessels within the model. The models used are given in equations (5.1) and (5.2) for both vessel groups.

$$\log_e\left(\frac{catch}{hours}\right) = \mu + \beta_{Observer} + \alpha(Hauls) + \varphi_{Year} + \phi_{Month} + \gamma_{CatchCategory} + v_{vessel} + \varepsilon \tag{5.1}$$

$$\log_e(catch) = \mu + \beta_{Observer} + \log_e(Hours) + \varphi_{Year} + \phi_{Month} + \gamma_{CatchCategory} + v_{vessel} + \varepsilon \tag{5.2}$$

where $v_{vessels}$ is a separate factor for each vessel making catches with levels for each of the 16 steel vessels and 55 ordinary vessels.

5.3. Results

The results for an application of equations (5.1) and (5.2) to ordinary and steel vessels data are given in Tables 5.1 and 5.2. The main effects alone are fitted first, then an interaction between the observer factor and month. From the interaction of the observer factor and month, the observer factor is redefined to show the size of the effect over different periods of the year.

It is clear from the results in Table 5.1 (for steel vessels) that, similar to Table 4.3 for all vessels (combined), observers have a large positive effect on catch rates between December and May and small effect between June and November, for sardine. The effect on catch rates for anchovy is high between May and October but less between November and April. Results in Table 5.2 (for ordinary vessels) are broadly very similar to these for steel vessels when monthly patterns are aggregated into six-monthly periods.

Table 5.1: Estimates of the observer effect for steel vessels (together with their standard errors) for $\log_e(CPUETS)$ and $\log_e(catch)$ models for both sardine and anchovy. For each type of there are three scenarios: the first occurs when only the main factors were fitted into the model; the second occurs when the observer effect differs for each month (i.e. an interaction between the observer factor and month); the last scenario occurs when the month factor is aggregated to show the effect of an observer between December to May and June to November for sardine, and between May to October and November to April for anchovy.

		Sardine	
		log(CPUETS)	log(catch)
	Month	Observer	Observer
No interactions		**0.14** (0.09)	-0.016(0.042)
Interaction	Jan	0.18 (0.55)	-0.17(0.25)
	Feb	0.79 (0.54)	**0.51**(0.21)
	Mar	0.32 (0.49)	**0.53**(0.23)
	Apr	0.39 (0.38)	0.05(0.34)
	May	0.36 (0.38)	0.20(0.28)
	Jun	0.19 (0.28)	0.38(0.22)
	Jul	-0.27(0.25)	-0.12(0.30)
	Aug	0.08 (0.40)	-0.95(0.98)
	Sep	0.12 (0.18)	**-0.39**(0.11)
	Oct	0.20 (0.25)	0.02(0.08)
	Nov	-0.01(0.26)	-0.06(0.07)
	Dec	0.42 (0.37)	**0.27**(0.13)
Aggregation	Dec-May	**0.40** (0.18)	**0.26**(0.09)
	Jun-Nov	0.06(0.10)	**-0.09**(0.05)
		Anchovy	
		log(CPUETS)	log(catch)
	Month	Observer	Observer
No interactions		**0.14** (0.04)	**0.22**(0.05)
Interaction	Jan	-0.89(0.49)	-3.95(11.81)
	Feb	-0.93(0.60)	-4.75(24.18)
	Mar	0.03(0.07)	0.05(0.09)
	Apr	-0.19(0.19)	-0.63(0.33)
	May	0.31(0.18)	0.11(0.23)
	Jun	0.21(0.11)	**0.41**(0.08)
	Jul	0.08(0.11)	**0.31**(0.09)
	Aug	**0.24**(0.11)	**0.58**(0.05)
	Sep	0.03(0.07)	0.05(0.09)
	Oct	**0.34**(0.10)	0.15(0.09)
	Nov	0.07(0.17)	-1.31(1.38)
	Dec	0.03(0.07)	0.05(0.09)
Aggregation	May-Oct	**0.16**(0.04)	**0.26**(0.05)
	Nov-Apr	0.00(0.10)	**-0.72**(0.34)

Table 5.2: Estimates of the observer effect for ordinary vessels (together with their standard errors) for $\log_e(CPUETS)$ and $\log_e(catch)$ models for both sardine and anchovy. For each type of species there are three scenarios: the first occurs when only the main factors were fitted into the model; the second occurs when the observer effect differs for each month (i.e. an interaction between the observer factor and month); the last scenario occurs when the month factor is aggregated to show the effect of an observer between December to May and June to November for sardine, and between May to October and November to April for anchovy.

Sardine			
		log(CPUETS)	log(catch)
	Month	Observer	Observer
No interactions		0.089 (0.087)	**0.21** (0.05)
Interaction	Jan	1.52 (1.39)	**1.28** (0.62)
	Feb	**1.01**(0.48)	**1.02**(0.16)
	Mar	0.15(0.30)	**0.30**(0.15)
	Apr	**1.24**(0.31)	**0.63**(0.17)
	May	0.46(0.27)	0.37(0.15)
	Jun	0.18(0.26)	**0.52**(0.13)
	Jul	**-0.77**(0.34)	-0.92((0.57)
	Aug	**-1.61**(0.32)	-0.66(0.20)
	Sep	-0.04(0.07)	0.01(12)
	Oct	0.15(0.25)	0.15(0.09)
	Nov	0.06(0.38)	0.12(0.09)
	Dec	0.31(0.99)	0.20(0.14)
Aggregation	Dec-May	**0.46** (0.10)	**0.53** (0.07)
	Jun-Nov	-0.21(0.09)	0.00 (0.06)
Anchovy			
		log(CPUETS)	log(catch)
	Month	Observer	
No interactions		**0.10** (0.04)	**0.084** (0.027)
Interaction	Jan	1.92 (1.11)	1.37(4.10)
	Feb	**2.13**(0.65)	1.24(1.65)
	Mar	-0.08(0.38)	-1.22(0.64)
	Apr	-0.38(0.25)	-0.03(0.19)
	May	0.26(0.20)	0.24(0.16)
	Jun	0.02(0.19)	0.06(0.14)
	Jul	0.47(0.24)	0.45(0.34)
	Aug	0.21(0.20)	0.09(0.14)
	Sep	-0.02(0.07)	-0.00(0.04)
	Oct	0.13(0.07)	0.14(0.13)
	Nov	0.86(0.32)	0.06(0.84)
	Dec	-0.02(0.07)	-0.00(0.04)
Aggregation	May-Oct	**0.11**(0.04)	**0.10**(0.03)
	Nov-Apr	-0.11(0.17)	-0.13(0.14)

CHAPTER 6

DIAGNOSTICS FOR THE MODELS CONSIDERED

Diagnostics were investigated for the models with a month-aggregated interaction effect and including all vessels (Figs 6.1-6.4) for both sardine and anchovy. In Fig. 6.1 the mean of standardised[2] residuals (for $\log_e(CPUETS)$) or deviance[3] residuals (for $\log_e(catch)$), henceforth termed residual means, are plotted against both month and hauls for sardine. The residual means do not seem to show any appreciable trend in relation to month that might suggest a model misspecification. Residual means against hauls seem to have somewhat similar behaviour, with instances of more than 5 hauls generally manifesting negative residuals.

Fig. 6.2 shows plots of the standard deviations of the residuals described above (henceforth termed residual standard deviations) against month and against hauls for both models for sardine. The residual standard deviations seem to be reasonably constant for both models and slightly steadier for the $\log_e(catch)$ model for both month and the haul factors.

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[2] Standardised residuals refer to the model residuals divided by the standard deviation of the set of residuals under consideration.

[3] Deviance residual refers to residuals from a Poisson error model, which is twice the difference between the maximum achievable log likelihood and that attained under the fitted model.

Fig. 6.3 shows the plots of residual means for $\log_e(CPUETS)$ and $\log_e(catch)$ models for anchovy. Again neither model seems to show any appreciable trend that could suggest serious model misspecification. In Fig. 6.4 residual standard deviations are plotted against month and hauls. In this case the $\log_e(catch)$ model again seems to show slightly more constant residual variance than the $\log_e(CPUETS)$ model.

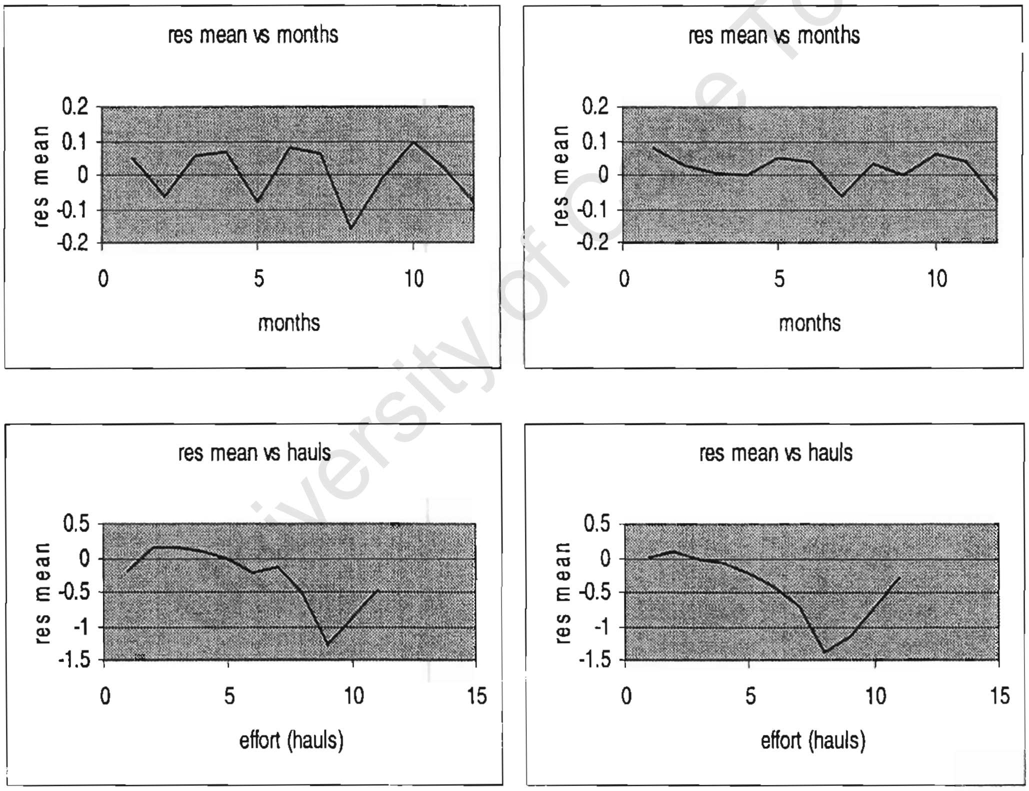

Figure 6.1: The means of standardised residuals or deviance residuals plotted against month and hauls (upper and lower panels respectively) for the $\log_e(CPUETS)$ (left side plots) and $\log_e(catch)$ (right side plots) models respectively, for models for **sardine** with

observer-aggregated month interactions. Values for each month or effort category are linked by straight lines.

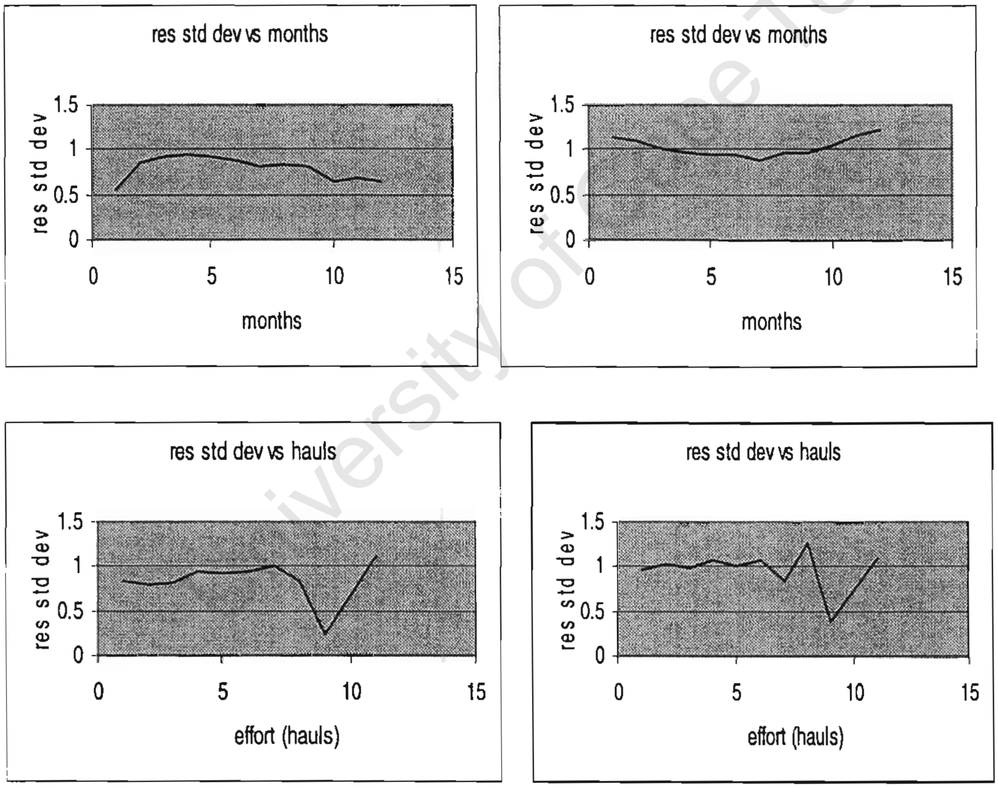

Figure 6.2: The standard deviations of the residuals considered in Fig. 6.1 plotted against month and hauls (upper and lower panels respectively) for the $\log_e(CPUETS)$ (left side plots) and $\log_e(catch)$ (right side plots) models for sardine for observer-aggregated month interactions.

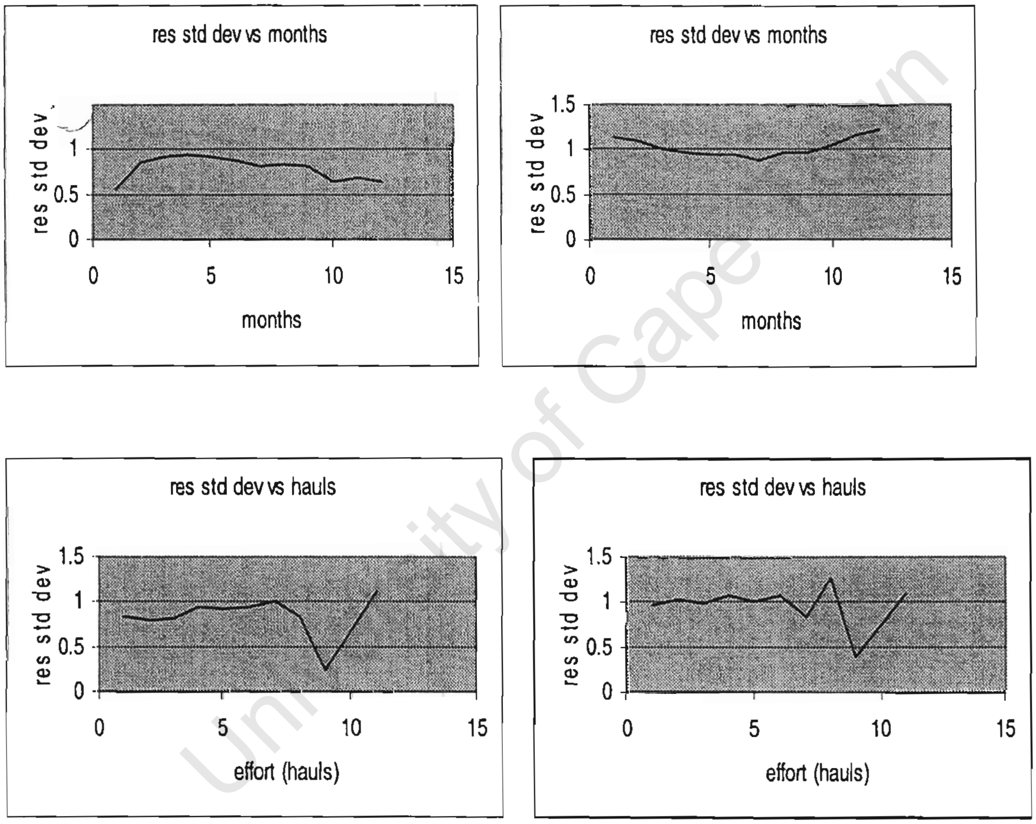

Figure 6.3: The means of standardised residuals or deviance residuals plotted against month and hauls (upper and lower panels respectively) for the $\log_e(CPUETS)$ (left side plots) and $\log_e(catch)$ (right side plots) models respectively, for models for **anchovy** with observer-aggregated month interactions.

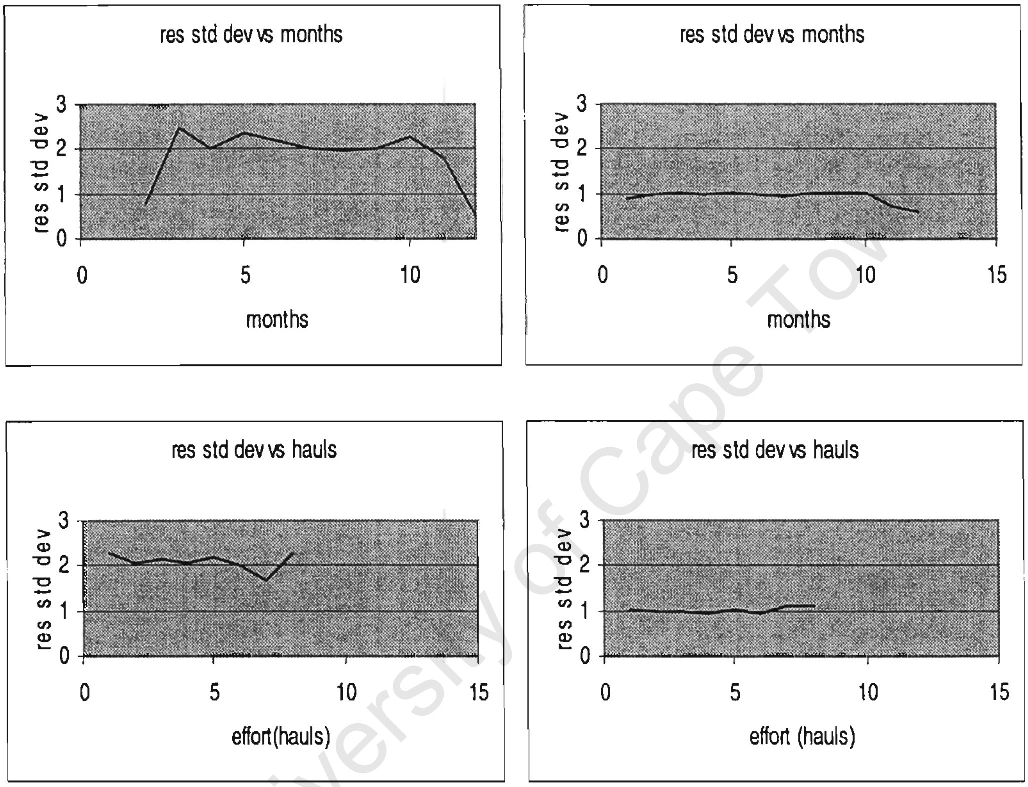

Figure 4: The standard deviations of the residuals considered in Fig. 6.1 plotted against month and hauls (upper and lower panels respectively) for the $\log_e(CPUETS)$ (left side plots) and $\log_e(catch)$ (right side plots) models for sardine for observer-aggregated month interactions.

CHAPTER 7

CONCLUSIONS

The GLM analyses of catch per time at sea (Table 4.3 of Chapter 4) indicate clearly that the placement of an observer on vessels fishing for sardine over the period January to June is linked to higher catches rates. However, for the period July to December the presence of observers on these vessels has little, if any, effect on these rates. These results are broadly the same when using both log normal and Poisson error models: at certain times of the year vessels with observers have higher sardine catch rates. This higher catch rates when observers are present in turn raises questions about the behaviour of at least some vessels when observers are not on board: are the catch rates lower because of dumping of fish?

For vessels fishing for anchovy, the presence of observers seems to impact catch rates over the period May and September. The log normal model indicates that catch rates for anchovy increase by approximately 10% when observers are on board these vessels, whereas the Poisson models indicate about twice that amount (approximately 20%). The presence of observers has no statistically significant impact over the period from October to April on vessels fishing for anchovy.

On the other hand, when catch rates are considered in the form of catch per haul (Table 4.4 of Chapter 4), the quantitative impacts of the presence of observers are estimated to be much less than indicated in Table 4.3. An exception is for sardine when using a log normal model over the period January to June, where the observer effect is higher at approximately 20 % but still lower than that the comparative estimate in Table 4.3. However, for the reasons given in section 4.7 of Chapter 4 (essentially greater reliability of the data and less potential for bias being introduced through other effects which influence haul size), the results of Table 4.3 based on catch per time at sea are considered more reliable.

Differentiating between ordinary and steel vessels (see, Tables 5.1 and 5.2 of Chapter 5) makes little impact on these results.

Based on the standardised residuals and deviance residual plots of Chapter 6, the Poisson error model for $\log_e(catch)$ seems slightly preferred because its steadier residual variances are more in accord with estimation assumptions than the log normal error model for $\log_e(CPUETS)$.

In summary, the analyses carried out for this study indicate broadly that when observers are on board pelagic fishing vessels catch rates are higher (though only for particular periods of the year) compared to those for vessels without observers. These discrepancies in catch rates may indicate that dumping is taking place when observers are not present. Based on the results from the Poisson error model for $\log_e(catch)$ the magnitude of the observer effect (and hence possible dumping) could be some 60%(point estimate 65%, 95% CI [48%; 84%])[4]for sardine catches made between January and June, and some 20%

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[4] These values follow from exponentiation of the parameter estimates shown in Table 4.3, and taking ± double the standard error to reflect a 95% confidence interval (CI) range.

(point estimate 22%, 95% CI [16%; 29%]) for anchovy catches between May and October.

CHAPTER 8

AREAS FOR FURTHER WORK

The GLM study of catch per hour applied to data for sardine and anchovy to determine observer effects have suggested statistically significant increases in the catch rate with observers on the vessels over January to June for the sardine fishery, and over May to October for the anchovy fishery. The differences in catch rates in turn has raised the possibility that the GLM technique may reflect and provide quantification of the extent of dumping in the catching operations conducted without observers present.

In a presentation of these results to the South African Inshore Fishing Industry Association, concerns were raised about the absence of a port factor in the GLMs used to estimate these observer effects. The example quoted was that for a port such as Hout Bay, vessels take shorter times to steam to the fishing grounds, so that use of catch per hour at sea as an intended comparable measure of fish density would be confounded.

The port factor was not included in the GLM analyses because this information is not routinely recorded by inspectors. Use of the port of registry for the vessel was considered, but rejected because it was clear from the observer data that in many cases vessels leave from one port but return to another.

Although port information is not recorded for trips, the times of hauls are recorded in addition to those of leaving and returning to port. Some measure of travelling time to and from the fishing grounds can thus be generated for each trip using the times recorded for the first and the last haul. This allows computation (by subtraction) of the time spent between hauls which provides a better basis to calculate catch per hour measures more likely to index fish density. However, the MCM (Marine and Coastal Management, South Africa) manager of the database for the pelagic fishery has recently expressed concerns about the accuracy of some of the haul times recorded, and revalidation of these data is currently in progress. Once this exercise has been completed, this study will need to be repeated using revalidated fishing time to see if taking account of travelling time to the fishing grounds in this way leads to any appreciable changes to the results.

Although no serious model misspecification has been suggested by the residual plots for the GLM analyses conducted, it could still be argued that catches made by the vessels are unlikely to be independent as assumed for the GLMs. The reason for non-independence may be because measurements (catches in this instance) are made repeatedly on the same vessels, (see Fig. 8.1). The data should thus be treated as if they are from an experiment with repeated measures where each subject (vessel in this instance) is observed over a period of time. The catches depicting clear trend over time as in Fig. 8.1 may suggest that time series models be considered.

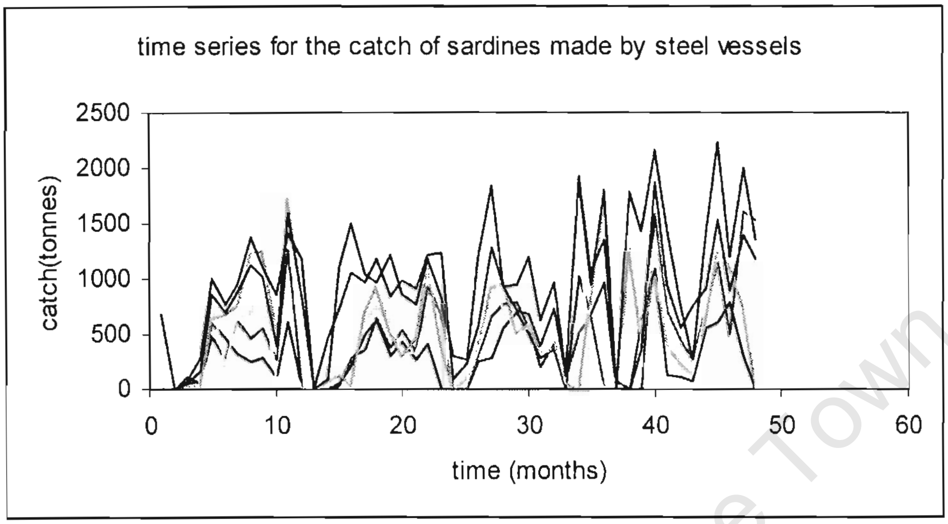


Figure 8.1: Time series of sardine catches made by six steel vessels from 1999 to 2002. The plot shows some seasonality in the trends of the catches, and some correlation between the catches made by the different vessels considered is also evident.

Lack of independence, both in repeated measures from the same vessel over time, and in measures at the same time by different vessels, would have the effect that the observer factors estimated in earlier Chapters are less precise than has been reported.

SECTION B:

WHAT IS THE POTENTIAL FOR THE CONSTRAINTS ASSOCIATED WITH *ECOPATH* TO IMPROVE ESTIMATES OF BIOMASS AND PRODUCTIVITY IN THE SOUTHERN BENGUELA?

CHAPTER 9

INTRODUCTION

The rise in the use of ECOPATH with ECOSIM (EwE) (Christensen *et al.* 2004) in ecology and the attempt to use it to analyse fisheries around the world has raised a number of fundamental research questions associated with different components of EwE. The three components of EwE described in Christensen *et al.* (2004) are ECOPATH, a static snapshot of the system; ECOSIM, a time-dynamic simulation for policy exploration; and ECOSPACE, a spatial temporal dynamic module primary designed to explore the impact and placement of protected areas. This study concentrates exclusively on the ECOPATH component of EwE. The fundamental question addressed is whether the constraints associated with the mass-balanced ECOPATH equations are capable of improving estimates of biomass and productivity. The southern Benguela region is used as an example.

The southern Benguela ecosystem extends from 29° S on the west coast of South Africa to 28° E on the east coast, and offshore to approximately 500-m depth contour, covering 220 000 km^2. The southern Benguela includes the upwelling region along the south-western coast of the continent, but also extends over the Agulhas Bank along the south coast (Shannon 2001) (see Fig. 9.1).

Shannon (2001) investigated components of the southern Benguela ecosystem with the intention of establishing a balanced southern Benguela ecosystem model for the system given data collected from different sources. The study spanned two periods

1980-1989 and 1990-1997. The main thrust of the study was the use of the "multiple-species" modelling technique ECOPATH to assess the trophic state of the southern Benguela. The different states of the two species, anchovy and sardine (which provide the basis for important purse-seine commercial fisheries), were assessed over these two periods with the aim of exploring the possibility of a regime shift between the two in terms of abundance.

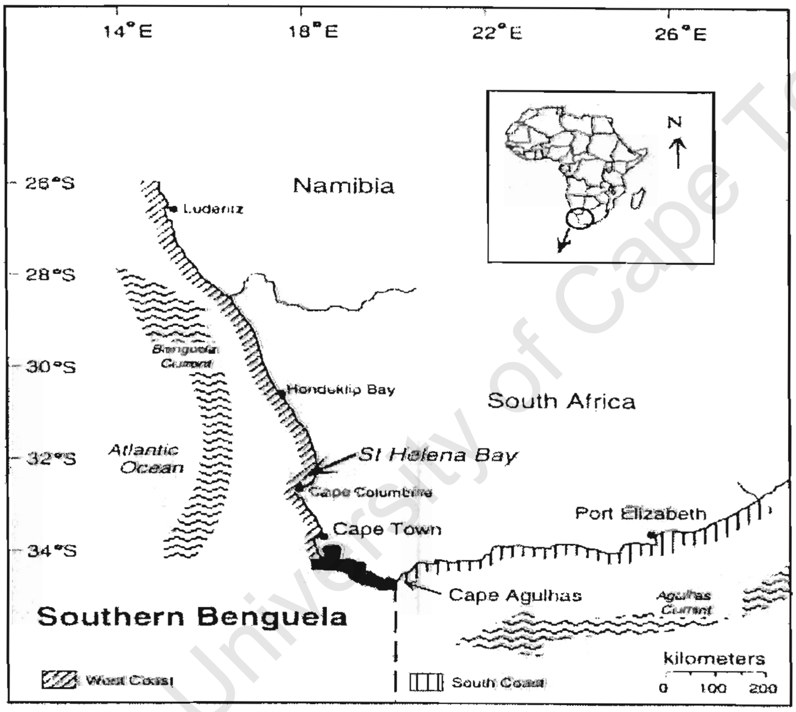


Figure 9.5: Conceptual map for the Southern Benguela upwelling system (from Plagányi 1995).

A potential criticism of single-species assessments is that they are typically based upon data pertaining only to the species under consideration. Yet this species exists in an ecosystem, and must also be bound by some general principles that apply to predator-prey relationships: for example, predators cannot consume prey at a faster rate than the prey mortality rate, and the mass conversion efficiency in this interaction (changing prey biomass consumed into predator somatic growth and reproductive output) must be subject to some upper bound. Can the application of such constraints improve the information needed (such as biomass estimates) for the provision of management advice related to target species?

Given the absence of a limit regarding the number of species that can be included in an ECOPATH model and the tendency of practitioners to create more complex models to take better account of biology underlying the system, there is sometimes a little or no due regard for the availability of the data to support such complex ecosystem models. The inevitable end result is an increase in scientific uncertainties, as a result of both absence of knowledge of functional relationships, and imprecision in estimates of the associated parameter values (Plagányi and Butterworth 2004). The imprecision in estimates of parameters is largely due to uncertainties in data, so any greater understanding of the likely values of the parameters calls for integration of uncertainties over all parameters (higher dimensional integration) of interest while imposing appropriate constraints (in this case those associated with ECOPATH).

The following simple example shows how such an approach might (or might not) assist. Assume single species assessments yielded abundance estimates for two species (P and Q) correct to ±20%. The actual state of this two-species complex could then lie anywhere within the shaded region in Fig. 9.2, which reflects all possibilities bounded by ± 20% of the best estimates $\hat{B}_P$ and $\hat{B}_Q$.

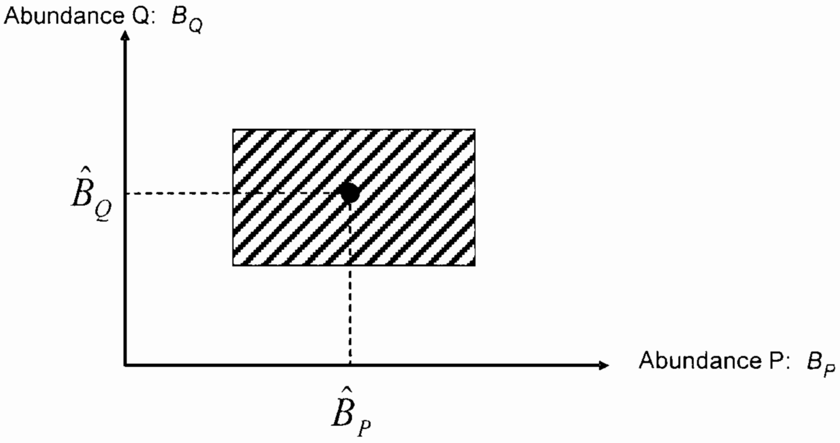


Fig. 9.2 The actual feasible parameter region for two species P and Q, with respective to the best abundance estimates $\hat{B}_P$ and $\hat{B}_Q$

Suppose now two predator-prey relationships provide the constraints shown in Fig. 9.3:

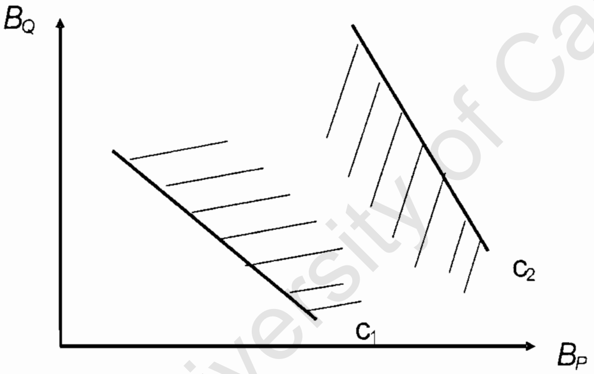


Fig. 9.3: The area of feasible region when bounded by two constraints C_1 and C_2

Only biomass combinations to the upper right of line C_1 and to the lower left of line C_2 are consistent with this extra information. Two possibilities can then occur, as illustrated in Figs 9.4 and 9.5:

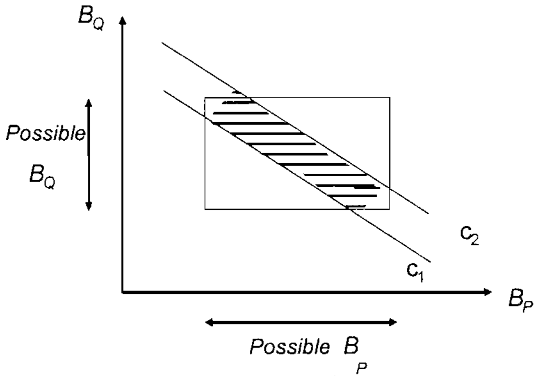


Fig. 9.4 No updating occurred

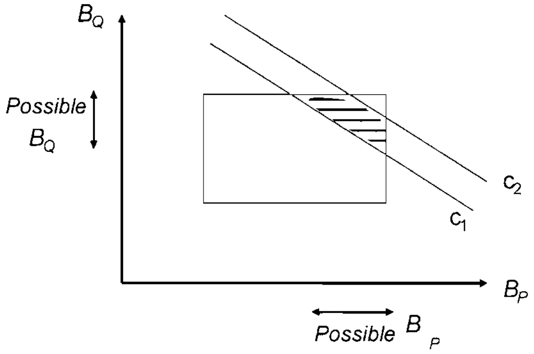


Fig. 9.5 Updating has taken place

In both cases, the area of feasible shaded region is much reduced, but the implications for improved knowledge about the biomasses of the two species treated individually are very different. In the Fig. 9.4 situation, there is no improvement: B_P remains equally likely to be anywhere within 20% of its single-species estimated value; all that the constraints achieve is to introduce a negative correlation between the B_P and B_Q estimates.

However, in the Fig. 9.5 situation, there is an improvement: both P and Q are shown to have to lie in the upper parts of their original uncertainty ranges.

It is clear from the preceding example that what is required is multi-dimensional equivalents of Figs 9.2-5 to explore whether inputs distributions for the biomass and productivity parameters of the southern Benguela ecosystem are narrowed by the imposition of the constraints associated with ECOPATH.

CHAPTER 10

BACKGROUND TO ECOPATH MODEL EQUATIONS

10.1. Introduction of ECOPATH

An ECOPATH model is a system of linear equations describing the average flows of mass (or energy) between species groups over a specified period of time (Christensen *et al.* 2000). Some elements of ECOPATH were introduced in the early 1980s (see Polovina 1984). A "mass balanced" ECOPATH has since been improved, relaxing some of its earlier redundant "steady state" assumptions (Pauly *et al.* 2000). "Mass balance" means that the model parameters describing an ecosystem obey the physical constraints that the total flow of mass (or energy) into each species group must equal the flow out of that group. In other words, ECOPATH models obey the first law of thermodynamics that mass and energy are conserved within a closed system (Kavanagh 2002). The "equilibrium"/ "steady-state" requirements of ECOPATH models (and subsequent relaxations thereof) mean that the model outputs apply only to the period for which the inputs are deemed valid (Christensen and Pauly 1992).

10.2. ECOPATH Equations

The full details of the EwE modelling approach, which has ECOPATH as its basis, are documented in numerous manuals and user guides accompanying the software. The latter is obtainable from the website www.ecopath.org. ECOPATH provides a mathematical basis for specifying the predator-prey-associated constraints on all the species in an ecosystem. The fundamental ECOPATH mass balance equation is based on that originally proposed by Polovina (1984). The basic derivation of the mass balance equations can be found in the manual accompanying EwE version 5. The balance for each functional group *i* in an ecosystem (detritus excluded) is described by:

$$B_i.(P/B)_i.EE_i = Y_i + \sum_j B_j.(Q/B)_j.DC_{ji} + BA_i + E_i \qquad (10.1)$$

or more conveniently

$$B_i.(P/B)_i.EE_i = \sum_j B_j.(Q/B)_j.DC_{ji} + EX_i \qquad (10.2)$$

where B_i and B_j are biomasses (the latter pertaining to *j*, the consumer of *i*);

$(P/B)_i$ is the production:biomass ratio for *i*,

EE_i is the fraction of production for *i* that is consumed within, or caught from the system (the balance being assumed to contribute to detritus);

Y_i is the fishery catch ($Y_i = FB$; F is the proportion fished);

$(Q/B)_j$ is the food consumption per unit biomass of *j*;

DC_{ji} is the fractional contribution by mass of *i* to the diet of *j*;

BA_i is a biomass accumulation term that describes a change in biomass over the time period studied and/or net migration (Christensen 1995);

$EX_i = Y_i + E_i + BA_i$ is the total export of group *i* out of the ecosystem; and

E_i is the net migration rate (emigration-immigration) of group *i* out of the ecosystem.

Equations (10.1) and (10.2) specify that the production achieved by a species must be balanced by the amount of that species consumed by others. Parameter values need to be chosen to satisfy the balance of these equations. Other associated equations are those describing ecotrophic efficiencies both for the living and detritus groups.

10.3. Ecotrophic Efficiency for Living Groups

The ecotrophic efficiency EE_i for group i is defined as the fraction of the group i production that is used in the ecosystem via consumption by other groups, biomass accumulation, fishing, or net migration out of the system (Kavanagh 2002). EE_i is also referred to as the ability to escape predation (Ernesto *et al.* 2004). For living groups, EE_i is calculated by solving equation (10.2) for EE_i:

$$EE_i = \frac{\sum_j B_j (Q/B)_j DC_{ji} + EX_i}{B_i (P/B)_i} \tag{10.3}$$

By definition EE_i is a fraction between 0 and 1. Values of EE_i greater than 1 mean that the input parameters are not biologically realistic although they do balance the equation mathematically. EE_i plays a crucial role when balancing the ECOPATH equations, particularly when the estimates of biomass, *P/B*, *Q/B* and diet composition data available for any given system do not lead to estimates of EE_i between 0 and 1 as required. If $EE_i > 1$ for any group, then it means that the predation and/or fisheries catches from the group in question exceeds its biological production. Balancing a model involves identifying such groups and changing input values to ensure that $0 < EE_i < 1$ (Kavanagh *et al.* 2004).

10.4. Ecotrophic Efficiency for Detritus Groups

To calculate the ecotrophic efficiency for the detritus groups, a slightly more complicated equation is used instead of equation (10.3). Kavanagh (2002) derives the equation for detritus groups as follows:

$$EE_i = \frac{DetEaten_i}{FlowIntoDet_i} \qquad (10.4)$$

$$DetEaten_i = \sum_j (B_j * (Q/B)_j * DC_{ji}) \qquad (10.5)$$

Equation (10.5) gives the sum of all detritus *i* eaten by predators *j*.

$$FlowIntoDet_i = \sum_k B_k (P/B)_k (1 - EE_k) DF_{ki} + \sum_k B_k (Q/B)_k GS_k DF_{ki} \qquad (10.6)$$

where:

DF_{ki} is detritus produced by each living group *i* going to each detritus group *k*, and

GS_k is the fraction of food not assimilated by organisms going to waste.

The first summation term in equation (10.6) represents dying organisms and the second represents the waste from living organisms. From equations (10.5) and (10.6) it follows that:

$$EE_i = \frac{\sum_j B_j (Q/B)_j DC_{ji}}{\sum_k B_k (P/B)_k (1 - EE_k) DF_{ki} + \sum_k B_k (Q/B)_k GS_k DF_{ki}} \qquad (10.7)$$

10.5. Parameterization of the ECOPATH model

10.5.1. Estimable parameters

For parameterization, ECOPATH sets up a theoretical system with as many linear equations as there are groups in a system (Christensen *et al.* 2002). An attraction of the ECOPATH approach is that for each species/species group, one of the quantities *B, P/B, Q/B* or *EE* is obtained by solving the linear equations and hence, given the other values needed, a unique mass-balance solution is easy to find (Plagányi and Butterworth 2004).

10.5.2. Input parameters

Other parameters required for calculation of the single unknown parameter for each species/species group are:

- Catch rates given as $Y_i = FB$ (where F is the proportion fished);
- Net emigration E_i;
- Biomass accumulation rate BA_i;
- Assimilation rate GS_i; and
- Diet composition DC_{ji}.

10.5.3. Constraints associated with ECOPATH

The fact that the ecotrophic efficiency must lie between 0 and 1 provides one key constraint that:

$$0 < EE_i < 1 \text{ for every species } i \tag{10.8}$$

The conversion efficiency $(P/Q)_i$ of food consumed is also a limiting factor. In this study, it is assumed that:

$$0 < (P/Q)_i < 0.6 \text{ for every species } i \tag{10.9}$$

where Q_i is the total mass of food consumed by species i.

$(P/Q)_i$ is typically considered to lie between 0.1 and 0.3 (see Shannon 2001).

CHAPTER 11

APPLICATION OF ECOPATH TO MODELS OF THE SOUTHERN BENGUELA ECOSYSTEM

11.1. Introduction

Substantial work on the application of ECOPATH models in the southern Benguela ecosystem has been carried out by Shannon (2001). This work has considered a number of broad research questions or issues relating to the Benguela ecosystem. These broad questions lead to key specific questions about components of the ecosystem. Amongst these broad questions/issues were:

1. Trophic flows in anchovy- versus sardine-dominated periods in the southern Benguela ecosystem. The issue of trophic flow leads further to, *inter alia*, the following specific questions:
    a) What were biomass, production, consumption and catches of the components of the southern Benguela system during the 1980s and 1990s?
    b) What is the primary production required to sustain the catches?
2. The potential use of "multi-species" approaches for management of resources in the Benguela upwelling region. This leads to the following questions amongst many:
    a) What can be learnt from the trophic models with regard to development of a "multi-species approach" to management of the Benguela ecosystem?
    b) What management advice can be given arising from these models and how can these models can be improved in future?

In summary the study by Shannon (2001) concerned assessing the state of the ecosystem by using ECOPATH with ECOSIM.

11.2. The Data

The data used by Shannon (2001) span two periods: 1980-1989 and 1990-1997. Full descriptions of the groups studied in the southern Benguela are discussed in Shannon (2001), with the sources of all data given in Appendix A thereof. The data used for this thesis were also provided by Shannon (pers. commn, Marine and Coastal Management (MCM), South Africa) and are given in Tables 11.1 and 11.2. These data represent a revised version of those appearing in Shannon (2001). The ranges set on input to establish ranges that give balanced models are given in Table 11.3. These ranges were used in Shannon (2001), and they are also used as inputs for this study. A particular combination of parameters was considered to be acceptable if it satisfied the criteria:

a) EE_i (ecotrophic efficiency) did not exceed 1.

b) Values of the model outputs were within user-defined ranges.

c) $(P/Q)_i$ values did not exceed 60% (0.6), the default value believed to be the ecologically acceptable maximum (Shannon 2001).

Table 11.1: Parameter values input for the southern Benguela ecosystem for the 1990s from Shannon (pers. commn, MCM, South Africa).

Group name	Biomass (t/km^2) *(B)*	Production/ biomass (/year) *(P/B)*	Consumption/ biomass (/year) *(Q/B)*	Ecotrophic efficiency *EE*	Production /consumption *(P/Q)*	Catch(t/km^2) *Y*
Phytoplankton	76.938	154.4	-	0.452	-	0
Microzooplankto	5.475	482	1928	0.999	0.25	0
Mesozooplankton	7.722	40	133.333	0.999	0.3	0
Macrozooplankto	13.067	13	31.707	0.999	0.41	0
Gelatinous zoop	5	0.584	1.669	0.152	0.35	0
Anchovy	3.573	1.4	14.4	0.878	0.097	0.812
Sardine	2.091	1.2	12.371	0.925	0.097	0.34
Redeye	5.289	1.3	13	0.99	0.1	0.234
Othersmallpel	0.364	1	10	0.875	0.1	0.001
Chubmackerel	0.455	0.9	9	0.55	0.1	0.033
Juvenilehorse	0.484	1.2	12	0.664	0.1	0.033
Adulthorse	1.937	1.5	10	0.496	0.15	0.106
Mesopelagic	9.176	1.2	12	0.999	0.1	0.003
Otherlargepel	0.468	0.494	5.168	0.833	0.096	0.11
Cephalopods	1.364	3.5	10	0.818	0.35	0.028
SmallM.capens	0.505	2.5	16.666	0.999	0.15	0.013
LargeM.capens	1.127	0.8	4.4	0.704	0.182	0.261
SmallM.parad	1.463	2.5	16.666	0.999	0.15	0.034
LargeM.parad	1.067	0.8	4.7	0.693	0.17	0.357
Pelagicdemers	4.381	0.7	3.5	0.999	0.2	0.057
Benthicdemers	3.385	0.7	3.5	0.999	0.2	0.054
Chondrichthyans	1.5	0.5	3.333	0.563	0.15	0.013
Seals	0.133	0.25	19.306	0.863	0.013	0.003
Cetaceans	0.1	0.15	10	0.999	0.015	0
Seabirds	0.012	0.123	118.269	0.963	0.001	0
Macrobenthos	56.109	1.2	10	0.837	0.12	0
Detritus	-	-	-	0.501	-	0

Table 11.2: Diet composition matrix for the southern Benguela ecosystem from 1990-1997 from Shannon (pers. commn, MCM, South Africa). The import term refers to additions from outside the ecosystem.

	diet Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	Phytoplankton		0.4	0.5	0.6		0.05	0.32																			
2	Microzooplankto		0.2	0.5			0.04	0.32																			
3	Mesozooplankton				0.4	0.64	0.57	0.29	0.6	0.81	0.05	0.75	0.39	0.4							0.01	0.01			0.035	0.009	
4	Macrozooplankto					0.12	0.34	0.07	0.4	0.16	0.66	0.25	0.52	0.6	0.095	0.27	0.729	0.1	0.769	0.21	0.645	0.05			0.035	0.096	
5	Gelatinous zoop					0.04				0.03																	
6	Anchovy										0.02		0.02		0.143	0.03	0.02	0.081	0.02	0.001	0.013	0.005	0.005	0.15	0.2	0.3	
7	Sardine										0.01		0.005		0.198	0.02	0.01	0.047	0.01	0.001	0.002		0.002	0.028	0.1	0.22	
8	Redeye										0.01		0.065		0.059	0.05	0.031	0.087	0.05	0.028	0.1	0.025	0.011	0.105	0.143	0.07	
9	Othersmallpel														0.032			0.01	0.001	0.002			0.005	0.003	0.037	0.06	
10	Chubmackerel														0.018			0.02					0.002	0.013		0.004	
11	Juvenilehorse														0.056			0.03						0.01		0.03	
12	Adulthorse														0.035			0.157					0.029	0.022	0.27		
13	Mesopelagic										0.25				0.106	0.1	0.078	0.1	0.08	0.364	0.15	0.05	0.065	0.007	0.04	0.103	
14	Otherlargepel														0.002			0.002		0.005			0.003	0.01		0.002	
15	Cephalopods														0.048	0.05	0.052	0.045	0.01	0.1	0.02	0.02	0.068	0.231	0.1	0.065	
16	SmallM.capens														0.026	0.022		0.11			0.004	0.001		0.1	0.004		
17	LargeM.capens																	0.04				0.002	0.017	0.022	0.01		
18	SmallM.parad														0.103	0.078	0.021	0.15		0.145	0.016	0.008		0.1	0.017	0.029	
19	LargeM.parad																			0.02		0.002	0.011	0.018	0.009		
20	Pelagicdemers														0.055		0.049	0.01	0.05	0.03	0.03	0.02	0.049	0.035		0.007	
21	Benthicdemers																0.01	0.01	0.01	0.094	0.01	0.02	0.174	0.079			
22	Chondrichthyans																					0.005	0.07				
23	Seals																						0.004			0.004	
24	Cetaceans																						0.003				
25	Seabirds																									0.001	
26	Macrobenthos														0.01	0.38						0.782	0.482	0.065			0.07
27	Detritus		0.4			0.2																					0.8
	Import														0.015												0.13
	Sum	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 11.3: Ranges used to balance southern Benguela models for the 1990s during the ECORANGER exercise in Shannon (2001). Ranges appearing in bold are the ranges within which parameters are deemed acceptable. Ranges appearing in regular font indicate those from which input parameters can be sampled to give a balanced model.

Group	**B (t.km^{-2})**	**P/B (y^{-1})**
Phytoplankton	20%	30%
Benthic producers	Unrestricted	20%
Microzooplankton	**1.0-11.0** *"acceptable" range was 1.2-5.6 (1990s)*	10%
Mesozooplankton	**1.0-23.5** *"acceptable" range was 5.3-20.5 (1990s)*	50%
Macrozooplankton	**1.8-21.9** *"acceptable" range was 11.0-19,2 (1990s)*	10%
Gelatinous zooplankton	30% (B is poorly known)	30%
Anchovy	10%	10%
Sardine	10%	10%
Redeye	5.0-11.1	10%
Other small pelagics	20%	20%
Chub mackerel	30%	10%
Juvenile horse mackerel	**0.4-0.6** 20% of the minimum and maximum B estimate of the species	10%
Adult horse mackerel	**1.6-2.5** (1990s: adult B estimated to be 80% of minimum and maximum B estimated for the species)	0.52 y^{-1}-1.1 y^{-1}
Mesopelagics	**4.5-10.9**	10%
Snoek	1990s: **estimated**, maximum set to 4.0	20%
Other large pelagics	20%	10%
Cephalopods	30%	20%
Small *M. capensis*	**Minimum=0.3** maximum set to 4.0 *"Acceptable" range was 0.4-0.8*	10%
Large *M. capensis*	10%	10%
Small *M. paradoxus*	**Minimum=1.3** maximum set to 4.0 *"acceptable" range was 1.3-2.3 (1990s)*	10%
Large *M. paradoxus*	10%	10%
Pelagic demersals	**Maximum set to 20**	20%
Benthic demersals	**Maximum set to 20**	20%
Pelagic chondrichthyans	30% (B is poorly known)	20%
Benthic chondrichthyans	30% (B is poorly known)	20%
Apex chondrichthyans	30% (B is poorly known)	20%
Seals	10%	0.03 y^{-1}– 1.041 y^{-1}
Cetaceans	30% (B estimate unavailable)	20%
Seabirds	10%	10%
Meiobenthos	**Maximum set to 200**	20%
Macrobenthos	**Maximum set to 200**	20%

CHAPTER 12

THE USE OF BAYESIAN TECHNIQUES IN MAKING INFERENCES ABOUT BIOMASS AND PRODUCTION/ BIOMASS RATIOS

12.1. General introduction to Methodology used

The statistical techniques that are used in this study are *maximum likelihood estimation* and *Bayesian* estimation methods implemented using the Markov Chain Monte Carlo (MCMC) approach. In the implementation of these methods, *maximum likelihood* is associated with maximization or minimization problems, with estimates implicitly defined as the solutions of such problems. *Bayesian* methods (implemented through the general framework of MCMC) are associated more with integration problems hence explicitly define estimators as an integral (see Roberts and Casella 2004). The inferences about parameters are made from posterior distributions rather than from the integral itself (see text below). In a Bayesian framework, statistics of interest such as means, standard deviations and credibility intervals are associated with posterior distributions. The Monte Carlo Markov Chain method is used in this study to integrate uncertainty over all the biomass and production:biomass ratio parameters. Uncertainty regarding diet compositions is integrated over in a similar fashion. Marginal posterior distributions for each parameter are produced together with associated statistics such as the mean, credibility interval and standard deviation to measure the degree of improvement from initial prior distributions and data.

12.2. Modelling Approach

The modelling approach followed is Bayesian in nature; where for the model investigated there are 52 parameters to be estimated as follows:

$$\hat{\mathbf{B}} = \{\hat{B}_i \in \Re : \hat{B}_i > 0, \qquad i = 1,2,\cdots,26\} \qquad (12.1)$$

and

$$\widehat{(\mathbf{P/B})} = \{\widehat{(P/B)}_i \in \Re : \widehat{(P/B)}_i > 0, \qquad i = 1,2,\cdots,26\}. \qquad (12.2)$$

Prior information about these parameters is taken to be represented by uniform distributions about the estimated values (see section below).

Notation is now changed slightly in order to clearly show the applicability of Bayes' theorem in a more general way. The procedure is as follows:

$$\boldsymbol{\theta} = \{\theta_i \in \Re : \theta_i > 0 \qquad i = 1,2,\cdots 52\} \qquad (12.3)$$

where

$$(\theta_1, \theta_2, \cdots \theta_{26})^T = (\hat{B}_1, \hat{B}_2, \cdots \hat{B}_{26})^T \qquad (12.4)$$

and

$$(\theta_{27}, \theta_{28}, \cdots, \theta_{52})^T = (\widehat{(P/B)}_{27}, \widehat{(P/B)}_{28}, \cdots, \widehat{(P/B)}_{52})^T \qquad (12.5)$$

where T represents the transpose of the vectors.

The non-zero constraint imposed on θ_i in equation (12.3) is somewhat redundant since priors imposed on θ_i ensure that θ_i is non-zero. It is further assumed that the parameter space θ and all its functions are continuous. There are two probability-related functions that are most important for this analysis. First there is a probability function $P(\theta)$ which represents the prior, and may be interpreted as the probability density placed on each possible value of the parameter before collecting any new data (Qian *et al.* 2003). There is also a conditional distribution giving the relation between data and parameters in θ space, which is expressed as a relative probability function $L(D \mid \theta)$, called the *likelihood function*. The *likelihood function* is used to update the prior information on θ to account for the new data *(D)* provided.

Then by Bayes' theorem:

$$P(\theta \mid D) \propto P(\theta)L(D \mid \theta) \tag{12.6}$$

Bayes' theorem reflects how the prior information is modified by the likelihood function to yield the posterior distribution. If a normalization constant is introduced Bayes' theorem becomes:

$$P(\theta \mid D) = \frac{P(\theta)L(D \mid \theta)}{\int P(\theta)L(D \mid \theta)d\theta} \tag{12.7}$$

Generally what is of interest from Bayes' theorem is the expectation of a function of parameter θ, $f(\theta)$ evaluated over the posterior distribution as follows:

$$E[f(\theta) \mid D] = \frac{\int_\theta f(\theta)P(\theta)L(D \mid \theta)d\theta}{\int_\theta P(\theta)L(D \mid \theta)d\theta} \tag{12.8}$$

or

$$E[f(\theta) \mid D] = \int_\theta f(\theta)P(\theta \mid D)d\theta \tag{12.9}$$

In most cases these integrals are intractable, especially for high dimensions as for the case in this study. MCMC provides an efficient numerical method for evaluating these integrals.

12.3. Markov Chain Monte Carlo (MCMC) as the method for integration

The idea behind MCMC for Bayesian inference is to create a random walk or Markov process, that has $P(\theta \mid D)$ as its stationary distribution, and then to run the process for long enough so that the resulting sample closely approximates a sample from $P(\theta \mid D)$ (Qian *et al.* 2003). If samples are drawn from $P(\theta \mid D)$, then $E[f(\theta)]$ can be approximated by

$$E[(f(\theta)] \approx \frac{1}{n}\sum_{i=1}^{n} f(\theta_i) \qquad (12.10)$$

In this case the population mean is being approximated by the sample mean. When the samples are independent, the law of large numbers ensures that the approximation can be made as accurate as desired by increasing the sample size (Gilks *et al.* 1996).

Generally samples need not be independent as it is not feasible to draw independent samples from $P(\theta \mid D)$. However a Markov chain can be generated from each member of the set θ. Then the next state θ_{i+1} is sampled from a distribution $P(\theta_{i+1} \mid \theta_i)$ which depends only on the current state of the chain θ_i. The chain will eventually 'forget'' its initial state, and $P(\theta \mid D)$ will converge to a unique stationary distribution, which does not depend on i and its starting position (Gilks *et al.* 1996). From the chain a burn of, say, the first k values are discarded from the chain of length n and an estimator for expectations calculated using the equation

$$f = \frac{1}{n-k}\sum_{i=k+1}^{n} f(\theta_i). \qquad (12.11)$$

This process is effected by the MCMC Metropolis-Hastings algorithm which is responsible for creating the jump function required to move from the initial or current position. The general exposition of the Metropolis-Hastings algorithm can be found in Gilks *et al.* (1996), or for a more formal account and different variations of Metropolis-Hastings algorithm see Robert and Cassella (1999).

12.4. Priors on parameters

Equation (10.1) can be thought of as providing a set of linear equations to evaluate EE_i for every species *i*, given the data inputs. To ease the algebra and computational speed, in this study EE_i is treated as the unknown in equation (10.1) for every species and the remaining parameters are input. For clarity, notation is now changed back to the original elements of θ: B_i and $(P/B)_i$.

Since all parameter values input to equation (10.1) are uncertain, we assume that the uncertainty is reflected by a uniform distribution over $\pm 20\%$, $\pm 40\%$ and $\pm 60\%$ of the original estimate. In addition, ranges of acceptable values used for the ECORANGER application by Shannon (2001) were considered (see Table 11.3). Thus if $\pm 20\%$ uncertainty were to be assumed for all species *i*, the priors on the biomasses and *(P/B)* ratios would be:

$$B_i \text{ from } U\left[0.8\hat{B}_i \;\; ; \;\; 1.2\hat{B}_i\right]$$

$$(P/B)_i \text{ from } U\left[0.8(\widehat{P/B})_i \;\; ; \;\; 1.2(\widehat{P/B})_i\right] \qquad (12.12)$$

Dietary proportion uncertainty is treated similarly except that when pseudo-data are generated from the uniform distributions in the MCMC computations, they need to be renormalized to ensure that the sum of the pseudo-proportions for the different species adds to unity.

Every set of generated pseudo-data and pseudo-proportions is then used to calculate EE_i for all species i from equation (10.1) and to compute $(P/Q)_i$; if, for any species, these results fail to satisfy constraints (10.8) and (10.9), the data-vector generated is rejected. Only vectors that satisfy *all* these constraints are retained. The marginal distributions provided by the retained vectors then provide "posterior" distributions to be compared with the input (in this example uniform) "priors". Comparison of posteriors with priors reveals whether the constraints have proved informative. Various permutations are investigated:

a) Uncertainties reflected by uniform distributions over $\pm 20\%$, $\pm 40\%$ and $\pm 60\%$ are introduced for original estimates of biomasses *(B)*, diet compositions and production:biomass *(P/B)* ratios. The aim is to assess what effect an increase in uncertainty has on the posterior distributions.

b) Uncertainty reflected by a uniform distribution over $\pm 40\%$ is introduced for original estimates of biomasses and production:biomass *(P/B)* ratios only, with diet values treated as certain (exact). The aim is to assess, if data for diet compositions for each species were known with a greater degree of certainty, whether there would be a difference compared to cases where there is large uncertainty in the diet data input.

c) Uncertainties reflected by a uniform distribution over ± 20%, ± 40% and ± 60% are introduced for the original estimates of biomass and diet values, here with the production:biomass *(P/B)* values treated as known and fixed.

The fixing of *(P/B)* is to ascertain whether there are any changes to the posterior distributions of the biomasses *(B)* compared to the case where the *(P/B)* are not fixed.

d) Uncertainties reflected by a uniform distribution over ± 60% are introduced for biomass *(B)*, production:biomass *(P/B)* ratios and diet, and in addition the uncertainty in the phytoplankton biomass is decreased to ± 10%. The aim is to check whether the possible low ability of the ECOPATH constraint equations to improve estimates of biomass *(B)* and perhaps *(P/B)* arises purely because wide ranges of inputs to the system at the lower level are otherwise considered possible.

12.5. Motivation for using Markov Chain Monte Carlo

ECOPATH with ECOSIM uses Monte Carlo integration (MCI) in its ECORANGER routine, which allows explicit consideration of uncertainty in input values (Pauly *et al.* 2000). There are, however, a number of problems with this approach when applied to a problem as big as the one considered. The following points are a motivation for using MCMC instead of the Monte Carlo integration based ECORANGER.

a) MCI over a strongly peaked function is computationally inefficient (Plagányi and Butterworth, 2004). In this study the problem of inefficiency arises because the large number of constraints imposed by the ECOPATH relations, such as that all EE_i parameters in the mass-balance equations must be less than 1, means that the feasible region is a very small proportion of the total parameter space.

b) If prior ranges are made very wide, MCI becomes very inefficient. If, on the other hand, prior ranges are made small there is a danger of excluding the regions that are important to sample. The difficulty imposed by these conflicting constraints is exacerbated by increase in dimensionality (Qian *et al.* 2003).

c) There is no guarantee that the posterior parameter space is sufficiently covered by the MCI; as a result marginal distributions of the posterior are not guaranteed to be accurate (Qian *et al.* 2003).

Markov Chain Monte Carlo overcomes the problems stated above because, *inter alia*, the most probable values of uncertain parameters do not have to be known exactly, thereby allowing prior ranges to be made wide to cover a larger plausible parameter space.

The approach used here to improve the efficiency of this computational process is carried out by fixing the "likelihood" to 1 if the vector generated from the priors satisfies all the constraints, and otherwise 0.

12.6. Technical considerations

The methodology above was implemented using the AD Model Builder (ADMB) (Otter Research LTD, 2000) package. The associated MCMC algorithm generates its jump function from the Hessian for a MLE process, which requires a likelihood that is not flat in the vicinity of the MLE (as is the "likelihood" posited above for all points in the feasible region). ADMB was therefore initially fed an additional pseudo-likelihood term with a maximum corresponding to the parameter estimates of Tables 11.1 and 11.2. Once the ADMB fitting process had converged to this MLE and evaluated a Hessian, and with it a jump function for the MCMC process, this additional pseudo-likelihood term was removed and the MCMC chain computations begun. In all cases chains of 1.5 and 3 million replicates were generated, saving every 1000th replicate, and analyses were conducted using the last thousand values of the resultant chain. The reason behind saving every 1000th replicate is to avoid autocorrelation. Exclusion of the beginning of the chain is to make sure that the independent sample is drawn from the stationary part of the chain only.

The ADMB software used is limited to no more than 250 parameters. Since there are 252 input values from which to sample when dietary uncertainty is considered, seven input values were fixed to bring the number of input parameters down to less than 250. To bring the fixed values to less than 250, values in the diet composition which had small estimates were fixed. Fixing these values was considered unlikely to have any appreciable influence in the overall computation of the other values.

CHAPTER 13

RESULTS

13.1. Markov Chains for the selected species

A single scenario is analyzed here (where ± 20 % uncertainty over biomass, production:biomass ratios and diet is assumed) as an illustration of the methodology used. A summary of other scenarios is presented in appendix A. Examples of chains produced during the computation of the Markov chain are given in Fig. 13.1 for selected species or groups. These chains exclude the burn-in period. All other calculations are based on these chains.

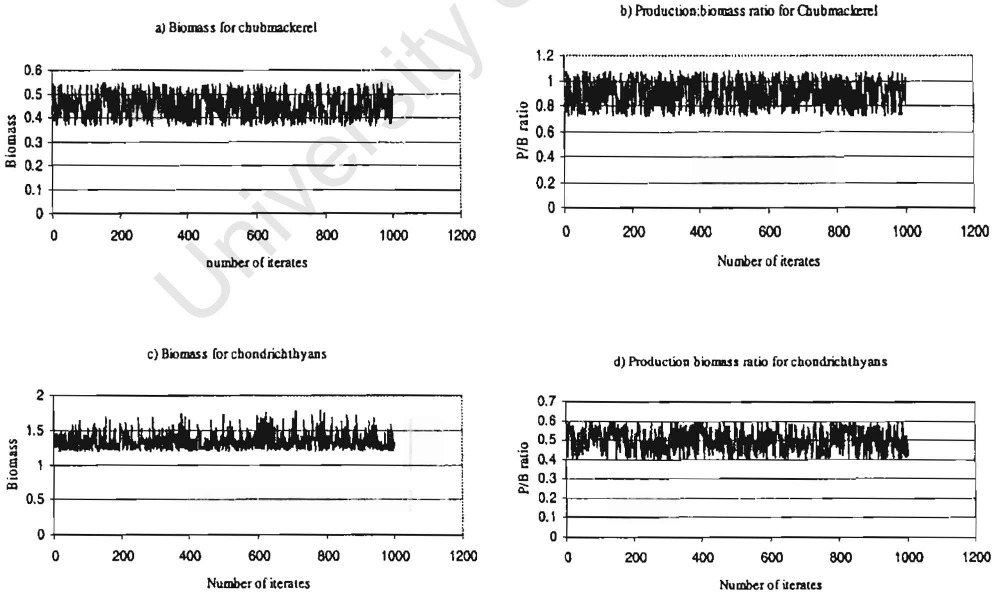


Figure 13.1: Typical results produced during computation of a Markov chain. The chains for the biomass and production:biomass ratio of the chubmackerel (a-b) and chondrichthyans (c-d) groups in the southern Benguela region are shown.

13.2. Convergence diagnostics

Convergence generally refers to the notion that the Metropolis-Hasting algorithm will eventually reach a stationary distribution, in which the distribution becomes stable in the parameter space. In this study a chain of 1.5 million was initially thought to be long enough to ensure convergence for all parameters. Although convergence seemed to have been achieved for 50 parameters (biomass and P:B ratios) from the plotted chain, it was clear that the chains for the biomasses for phytoplankton and sea birds were still showing some kind of trend. Longer chains (3 million) were then generated for priors (uniform over ± 20 %, ± 40 % and ± 60 % of input values) and the trace plots similar to those given in Fig. 13.1 were inspected. When there were no indications of trends in these plots, convergence was assumed to have occurred.

An alternative method to the trace plots was also considered whereby the sample from the posterior distribution is split in half and the means and standard deviations from each half were compared. If the means and standard deviations from each half were reasonably similar, that was deemed sufficient basis to assume convergence. Tables 13.1 and 13.2 give such results for biomasses and production:biomass *(P/B)* ratios respectively for the ± 20 % scenario, which are strongly suggestive of adequate convergence. More formal convergence tests could have been applied, but given that the intent of the computations was for qualitative more than quantitatively exact results, formal convergence tests were not pursued.

13.3. Table of results and posterior distributions

The case considered in this Chapter assumed a uniform multiplicative prior on [0.8**parameter*; 1.2* *parameter*] ("20 %") on all inputs. Sensitivities were conducted to alternative choices for this prior: these include a case where ("40%") uncertainty was applied to the *B* and *P/B* inputs only, with the diet proportions treated as exact (scenario (b) given in section 12.4 of Chapter 12); cases where ("20%", "40%" and "60%") uncertainty was applied to biomass and diet inputs with production:biomass ratios treated as exact (scenario (c) of section 12.4 of chapter 12); and a case where ("60%") uncertainty was applied to all inputs except phytoplankton where the uncertainty was set at ("10%") only.

Given the uncertainties (e.g. survey sampling variance alone) typical of marine resource abundance and productivity estimates, higher uncertainty (more than 20%) would constitute a more realistic reflection of the extent of input uncertainty. Tables 13.3 and 13.4 provide summary statistics showing the extent to which the posterior distribution has improved relative to the prior.

The most important measure of whether any improvement has been made is the standard deviation. As the standard deviation measures the spread of the distribution, a reduction in standard deviation gives an indication that prior information has been updated. The plot of the posterior distribution, represented by a probability density function, gives an indication of the likely values for a given parameter. Fig. 13.2 gives some examples of posterior distributions for the ± 20 scenarios

Table 13.1: The means and standard deviations for **biomass (B)** of the different ecotrophic groups. The chains were divided into two, following which the means and standard deviations of the first and second halves were calculated. Almost all the means and their standard deviations from the first half of the chain are the same as those from the second half of the chain (to two decimal places), which strongly suggests that the stationary distributions were reached for each species group.

	Mean from 1st half	Mean from 2nd half	Std dev from 1st half	Std dev from 2nd half
1 Phytoplankton	78.33	77.71	8.92	8.92
2 Microzooplankton	5.61	5.64	0.62	0.62
3 Mesozooplankton	8.31	8.30	0.66	0.65
4 Macrozooplankton	13.85	13.79	1.19	1.16
5 Gelatinous zooplankton	5.01	5.01	0.58	0.57
6 Anchovy	3.61	3.62	0.39	0.39
7 Sardine	2.19	2.18	0.22	0.22
8 Redeye	5.56	5.55	0.51	0.50
9 Othersmallpel	0.37	0.37	0.04	0.04
10 Chubmackerel	0.45	0.45	0.05	0.05
11 Juvenilehorse	0.48	0.48	0.05	0.05
12 Adulthorse	1.88	1.89	0.22	0.22
13 Mesopelagic	9.59	9.55	0.88	0.89
14 Otherlargepel	0.47	0.47	0.05	0.05
15 Cephalopods	1.30	1.30	0.14	0.14
16 SmallM.capens	0.53	0.52	0.05	0.05
17 LargeM.capens	1.05	1.05	0.11	0.11
18 SmallM.parad	1.46	1.46	0.14	0.14
19 LargeM.parad	1.01	1.01	0.11	0.11
20 Pelagicdemers	4.49	4.49	0.44	0.44
21 Benthicdemers	3.46	3.47	0.36	0.36
22 Chondrichthyans	1.33	1.34	0.12	0.12
23 Seals	0.13	0.13	0.01	0.01
24 Cetaceans	0.11	0.10	0.01	0.01
25 Seabirds	0.01	0.01	0.001	0.001
26 Macrobenthos	56.90	56.91	6.41	6.43

Table 13.2: The means and standard deviations for **production:biomass (P/B) ratios** of the different ecotrophic groups. The chains were divided into two, the means and standard deviations of the first and second halves were calculated. Almost all (except Phytoplankton) the means and their standard deviations from the first half of the chain are the same as those from the second half of the chain (to two decimal places) which strongly suggests that the stationary distributions were reached for each species group.

	Mean from 1st half	Mean from 2nd half	Std dev from 1st half	Std dev from 2nd half
1 Phytoplankton	162.97	156.25	18.40	18.80
2 Microzooplankton	523.36	521.41	30.75	28.73
3 Mesozooplankton	43.56	43.63	3.20	3.23
4 Macrozooplankton	14.12	14.13	1.09	1.08
5 Gelatinous zooplanktor	0.59	0.58	0.07	0.07
6 Anchovy	1.46	1.46	0.15	0.15
7 Sardine	1.25	1.25	0.12	0.12
8 Redeye	1.39	1.39	0.12	0.12
9 Othersmallpel	1.03	1.02	0.11	0.11
10 Chubmackerel	0.89	0.90	0.10	0.10
11 Juvenilehorse	1.21	1.21	0.14	0.14
12 Adulthorse	1.50	1.50	0.18	0.18
13 Mesopelagic	1.28	1.29	0.11	0.11
14 Otherlargepel	0.51	0.51	0.05	0.05
15 Cephalopods	3.62	3.63	0.36	0.36
16 SmallM.capens	2.64	2.65	0.24	0.24
17 LargeM.capens	0.80	0.80	0.09	0.09
18 SmallM.parad	2.70	2.72	0.21	0.21
19 LargeM.parad	0.80	0.80	0.09	0.09
20 Pelagicdemers	0.76	0.76	0.06	0.06
21 Benthicdemers	0.75	0.75	0.07	0.07
22 Chondrichthyans	0.50	0.50	0.06	0.06
23 Seals	0.26	0.26	0.03	0.03
24 Cetaceans	0.15	0.16	0.02	0.02
25 Seabirds	0.13	0.13	0.008	0.009
26 Macrobenthos	1.22	1.23	0.13	0.13

Table 13.3: Comparison of selected statistics for the prior (uniform over ±20% of input value – see Table 11.1) and posterior distributions of **production:biomass** ratios ***(P/B)*** for the different ecotrophic groups. In this and the following tables, relative changes have been computed as $\left(\frac{\text{post - prior}}{\text{prior}}\right)$, except for the lower 90% PI (probability interval) where these have been computed as $\left(\frac{\text{prior - post}}{\text{prior}}\right)$, so that negative relative changes in spread statistics are sign-consistent in indicating an improvement. For the averages, the four groups are as follows: "Planktonic and other" includes groups 1 to 5, and 26, "Pelagics" includes groups 7 to 14 , "Demersals" includes groups 16 to 21 and "Top predators" includes groups 22 to 25.

	Prior						Posterior							Relative changes (in %)					
			90% PI							90% PI						90%PI			
	median	stddev	lower	upper	width	CV	median	mean	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1 Phytoplankton	154.4	17.83	126.61	182.19	55.58	0.12	157.05	156.25	18.80	125.86	183.36	57.51	0.12	2	5	1	1	3	4
2 Microzooplankto	482	55.66	395.24	568.76	173.52	0.12	518.13	521.41	28.73	480.58	569.97	89.39	0.06	7	-48	-18	0	-48	-52
3 Mesozooplankton	40	4.62	32.80	47.20	14.40	0.12	44.18	43.63	3.23	37.64	47.71	10.07	0.07	10	-30	-13	1	-30	-36
4 Macrozooplankto	13	1.50	10.66	15.34	4.68	0.12	14.37	14.13	1.08	12.09	15.47	3.37	0.08	11	-28	-12	1	-28	-34
5 Gelatinous zoop	0.584	0.07	0.48	0.69	0.21	0.12	0.58	0.58	0.07	0.48	0.69	0.21	0.11	0	-2	0	0	0	-2
6 Anchovy	1.4	0.16	1.15	1.65	0.50	0.12	1.48	1.46	0.15	1.19	1.66	0.47	0.10	5	-9	-3	0	-6	-13
7 Sardine	1.2	0.14	0.98	1.42	0.43	0.12	1.26	1.25	0.12	1.03	1.42	0.40	0.10	5	-10	-4	1	-8	-13
8 Redeye	1.3	0.15	1.07	1.53	0.47	0.12	1.41	1.39	0.12	1.18	1.55	0.37	0.08	9	-23	-9	1	-21	-28
9 Othersmallpel	1	0.12	0.82	1.18	0.36	0.12	1.03	1.02	0.11	0.83	1.18	0.36	0.11	3	-4	-1	0	-1	-6
10 Chubmackerel	0.9	0.10	0.74	1.06	0.32	0.12	0.90	0.90	0.10	0.74	1.06	0.33	0.12	0	1	0	0	1	1
11 Juvenilehorse	1.2	0.14	0.98	1.42	0.43	0.12	1.22	1.21	0.14	0.99	1.42	0.43	0.11	2	-2	0	0	-1	-3
12 Adulthorse	1.5	0.17	1.23	1.77	0.54	0.12	1.50	1.50	0.18	1.23	1.76	0.54	0.12	0	2	0	0	-1	2
13 Mesopelagic	1.2	0.14	0.98	1.42	0.43	0.12	1.31	1.29	0.11	1.09	1.43	0.34	0.08	9	-21	-10	1	-21	-27
14 Otherlargepel	0.493	0.06	0.40	0.58	0.18	0.12	0.51	0.51	0.05	0.41	0.58	0.17	0.10	4	-8	-3	0	-6	-11
15 Cephalopods	3.5	0.40	2.87	4.13	1.26	0.12	3.65	3.63	0.36	2.99	4.15	1.16	0.10	4	-11	-4	1	-8	-14
16 SmallM.capens	2.5	0.29	2.05	2.95	0.90	0.12	2.69	2.65	0.24	2.18	2.97	0.79	0.09	8	-16	-6	1	-13	-21
17 LargeM.capens	0.8	0.09	0.66	0.94	0.29	0.12	0.80	0.80	0.09	0.65	0.94	0.29	0.12	0	2	1	0	1	2
18 SmallM.parad	2.5	0.29	2.05	2.95	0.90	0.12	2.77	2.72	0.21	2.32	2.98	0.66	0.08	11	-27	-12	1	-26	-33
19 LargeM.parad	0.8	0.09	0.66	0.94	0.29	0.12	0.80	0.80	0.09	0.65	0.94	0.29	0.12	0	0	0	0	0	0
20 Pelagicdemers	0.7	0.08	0.57	0.83	0.25	0.12	0.77	0.76	0.06	0.66	0.83	0.18	0.07	11	-31	-13	1	-30	-37
21 Benthicdemers	0.7	0.08	0.57	0.83	0.25	0.12	0.76	0.75	0.07	0.62	0.83	0.21	0.09	8	-19	-8	1	-17	-24
22 Chondrichthyans	0.5	0.06	0.41	0.59	0.18	0.12	0.50	0.50	0.06	0.41	0.59	0.18	0.12	-1	-1	0	0	-1	0
23 Seals	0.25	0.03	0.21	0.30	0.09	0.12	0.26	0.26	0.03	0.21	0.30	0.09	0.11	3	-5	-1	0	-2	-7
24 Cetaceans	0.15	0.02	0.12	0.18	0.05	0.12	0.16	0.16	0.02	0.13	0.18	0.05	0.10	6	-12	-5	0	-10	-16
25 Seabirds	0.123	0.01	0.10	0.15	0.04	0.12	0.13	0.13	0.01	0.12	0.15	0.03	0.06	9	-40	-16	1	-40	-45
26 Macrobenthos	1.2	0.14	0.98	1.42	0.43	0.12	1.23	1.23	0.13	1.02	1.42	0.40	0.10	2	-7	-3	0	-7	-9
Averages																			
Planktonic and other	115.20	13.30	94.46	135.93	41.47	0.12	122.59	122.87	8.67	109.61	136.44	26.83	0.09	5	-18	-8	0	-18	-21
Pelagics	1.37	0.16	1.12	1.62	0.49	0.12	1.43	1.42	0.14	1.17	1.62	0.46	0.10	4	-8	-3	0	-7	-11
Demersals	1.33	0.15	1.09	1.57	0.48	0.12	1.43	1.41	0.13	1.18	1.58	0.40	0.09	6	-15	-6	1	-14	-19
Top predators	0.26	0.03	0.21	0.30	0.09	0.12	0.26	0.26	0.03	0.22	0.30	0.09	0.10	4	-14	-5	0	-13	-17
Overall average	27.46	3.17	22.52	32.40	9.88	0.12	29.21	29.27	2.09	26.05	32.52	6.47	0.10	5	-13	-5	0	-12	-16

Table 13.4: Comparison of some statistics for the prior (uniform over ±20% of input value – see Table 11.1) and posterior distributions of **biomass *(B)*** for the different ecotrophic groups. For this and following tables, relative changes have been computed as $\left(\dfrac{\text{post - prior}}{\text{prior}}\right)$, except for the lower 90% PI where these have been computed as $\left(\dfrac{\text{prior - post}}{\text{prior}}\right)$, so that negative relative changes in spread statistics are sign-consistent in indicating an improvement. For the averages, the four groups are as follows: "Planktonic and other". includes groups 1 to 5, and 26, "Pelagics" includes groups 7 to 14 , "Demersals" includes groups 16 to 21 and "Top predators" includes groups 22 to 25.

		Prior						Posterior							Relative changes (in %)					
				90% PI							90% PI						90%PI			
		median	stddev	lower	upper	width	CV	median	mean	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	76.938	8.88	63.09	90.79	27.70	0.12	78.13	77.71	8.92	63.46	91.17	27.71	0.11	2	0	-1	0	0	-1
2	Microzooplankton	5.475	0.63	4.49	6.46	1.97	0.12	5.71	5.64	0.62	4.53	6.51	1.98	0.11	4	-2	-1	1	0	-5
3	Mesozooplankton	7.722	0.89	6.33	9.11	2.78	0 12	8.36	8.30	0.65	7.16	9.19	2.03	0.08	9	-27	-12	1	-27	-32
4	Macrozooplankton	13.067	1.51	10 71	15.42	4.70	0 12	13.88	13.79	1.16	11.76	15.62	3.76	0.08	6	-23	-9	1	-20	-27
5	Gelatinous zooplankton	5.000	0.58	4.10	5.90	1.80	0 12	5.04	5.01	0.57	4.12	5.89	1.77	0.11	1	-1	-1	0	-2	-1
6	Anchovy	3.573	0.41	2.93	4.22	1.29	0.12	3.64	3.62	0.39	2.98	4.22	1.24	0.11	2	-5	-2	0	-3	-6
7	Sardine	2.091	0.24	1.71	2.47	0.75	0.12	2.21	2.18	0.22	1.78	2.48	0.70	0.10	6	-9	-4	1	-7	-13
8	Redeye	5.289	0.61	4.34	6 24	1.90	0.12	5.59	5.55	0.50	4.70	6.28	1.58	0 09	6	-18	-8	1	-17	-22
9	Othersmallpel	0.364	0.04	0.30	0 43	0.13	0.12	0.38	0.37	0.04	0.30	0.43	0.13	0 11	3	-6	-2	0	-4	-8
10	Chubmackerel	0.455	0.05	0.37	0 54	0.16	0.12	0.45	0.45	0.05	0.37	0.54	0.16	0 12	-1	1	0	0	0	2
11	Juvenilehorse	0.484	0.06	0.40	0.57	0.17	0.12	0.48	0 48	0.05	0.40	0.57	0.17	0 11	0	-2	0	0	0	-2
12	Adulthorse	1.937	0.22	1.59	2.29	0.70	0.12	1.87	1.89	0.22	1.58	2.28	0.70	0.12	-4	-1	1	0	0	1
13	Mesopelagic	9.176	1.06	7.52	10.83	3.30	0 12	9.63	9.55	0.89	8.02	10.82	2.80	0.09	5	-16	-6	0	-15	-20
14	Otherlargepel	0.468	0.05	0.38	0.55	0.17	0 12	0.47	0.47	0.05	0.39	0.55	0.16	0.11	0	-5	-1	-1	-4	-5
15	Cephalopods	1.364	0.16	1.12	1.61	0.49	0.12	1.27	1.30	0.14	1.11	1.56	0.46	0.11	-7	-8	1	-3	-7	-3
16	SmallM.capens	0.505	0.06	0.41	0.60	0.18	0 12	0.52	0.52	0.05	0.44	0.60	0.16	0.10	4	-13	-5	0	-11	-15
17	LargeM.capens	1.127	0.13	0.92	1.33	0.41	0.12	1.03	1.05	0 11	0.92	1.28	0.36	0.11	-9	-14	1	-4	-11	-8
18	SmallM.parad	1.463	0.17	1.20	1.73	0.53	0.12	1.45	1.46	0.14	1.23	1.71	0.48	0 10	-1	-15	-3	-1	-10	-14
19	LargeM parad	1.067	0.12	0.87	1.26	0.38	0.12	0.99	1.01	0.11	0.87	1.23	0.37	0 11	-7	-7	1	-2	-5	-2
20	Pelagicdemers	4.381	0.51	3.59	5.17	1.58	0.12	4.51	4.49	0.44	3.74	5.15	1.41	0 10	3	-14	-4	0	-11	-16
21	Benthicdemers	3.385	0.39	2.78	3.99	1.22	0.12	3.49	3.47	0.36	2.87	4.00	1.14	0 10	3	-8	-3	0	-7	-11
22	Chondrichthyans	1.500	0.17	1.23	1.77	0.54	0.12	1.31	1.34	0.12	1.21	1.59	0.38	0.09	-13	-29	2	-10	-29	-21
23	Seals	0.133	0.02	0.11	0.16	0.05	0.12	0.13	0.13	0.01	0.11	0.15	0.05	0.11	-3	-5	1	-2	-3	-3
24	Cetaceans	0.100	0.01	0.08	0.12	0.04	0 12	0.11	0.10	0.01	0.09	0 12	0.03	0.10	6	-13	-4	0	-10	-17
25	Seabirds	0.012	0.001	0.010	0.01	0.004	0 12	0.01	0.01	0.00	0.01	0 01	0.00	0.11	-6	-10	1	-3	-8	-6
26	Macrobenthos	56.109	6.48	46.01	66.21	20.20	0.12	57.12	56.91	6.43	46.36	66.34	19.98	0.11	2	-1	-1	0	-1	-2
	Averages																			
	Planktonic and other	27.4	3.2	22.5	32.3	9.9	0 1	28.0	27.9	3.1	22.9	32.4	9.5	0 1	4	-9	-4	0	-8	-11
	Pelagics	2.6	0.3	2.2	3.1	1.0	0.1	2.7	2.7	0.3	2.3	3.1	0.8	0 1	2	-7	-2	0	-6	-8
	Demersals	2.0	0.2	1.6	2.3	0.7	0.1	2.0	2.0	0.2	1.7	2.3	0.7	0.1	-1	-12	-2	-1	-9	-11
	Top predators	0.4	0.1	0.4	0.5	0.2	0.1	0.4	0.4	0.0	0.4	0.5	0.1	0.1	-4	-14	0	-4	-13	-12
	Overall average	7.81	0.90	6.41	9.22	2.81	0 12	7.99	7.95	0.86	6.56	9.24	2.68	0.10	0	-10	-2	-1	-8	-10

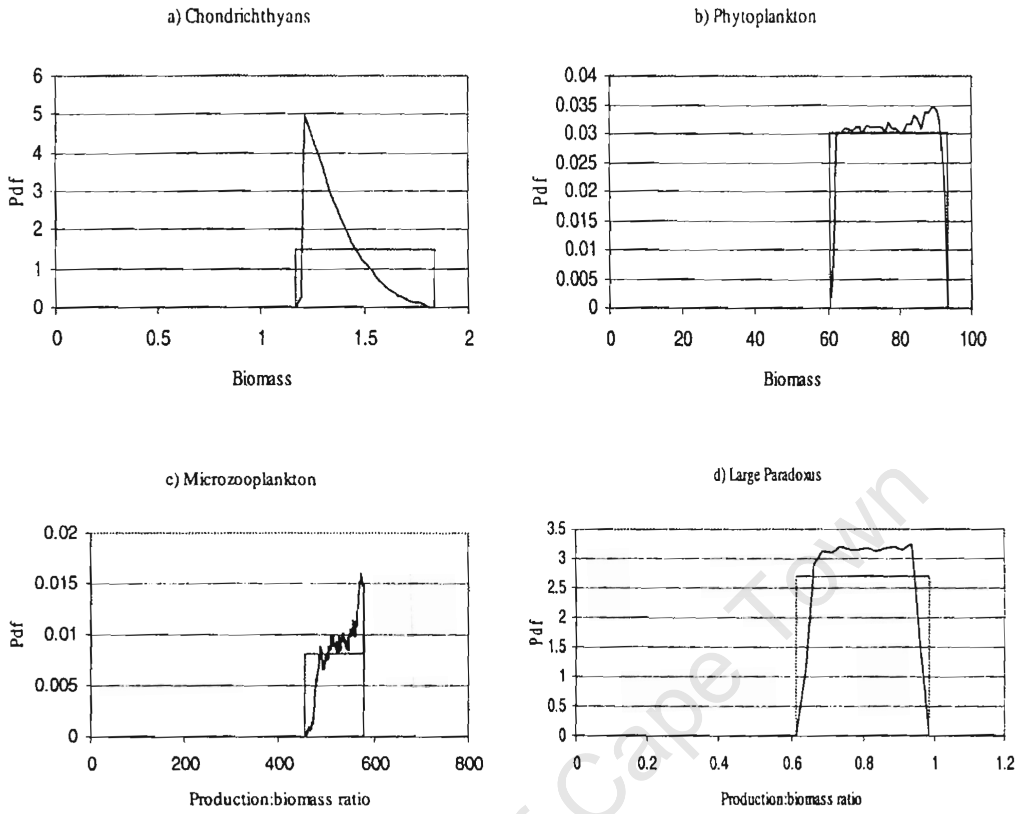


Figure 13.2: a-d. Prior (uniform over ±20% of input value) and posterior distributions for biomass *(B)* estimates (expressed in t/km^2) (Figs. a-b at the top), and production:biomass *(P/B)* ratios (expressed as yr^{-1}) (Figs. c-d at the bottom). Examples presented are for the species showing the greatest improvement in estimates precision: (a) and (c) (biomass of chondrichthyans and *(P/B)* ratios of microzooplankton) and the species showing the least improvement: (b) and (d) (biomass of phytoplankton and *(P/B)* ratio of large *M. paradoxus*).

CHAPTER 14

DISCUSSION

A summary of the results for scenarios specified in section 12.4 of Chapter 12 is given in Appendix A. These results show the extent to which the constraints imposed by the ECOPATH equations update the prior distributions for both biomasses *(B)* and production:biomass ratios *(P/B)*. In broad terms, for biomass these results suggest:

- That there is a general reduction in uncertainty as measured by standard deviation. The reduction is appreciably larger when the input uncertainties are increased from $\pm 40\%$ and $\pm 60\%$.
- However, this $\pm 60\%$ case aside, these improvements are not large, being typically less than 20% for most individual groups. The improvement of results is not large also when the groups are aggregated into four broad categories.
- When the uncertainty concerning the phytoplankton biomass is reduced to $\pm 10\%$, there is little improvement for most of the groups compared to the case in which the uncertainty is $\pm 60\%$ throughout.
- When the uncertainty ranges given in Table 11.3 (from Shannon 2001) are used, the reduction in these uncertainties overall averages to almost the same as for the $\pm 60\%$ case, but at a group level the reduction for the demersal group is greater but that for top predators less.

For the production:biomass ratios (*P/B*), reductions in the extent of uncertainty are somewhat larger (see Table A.2). To summarise:

- The decrease in uncertainty for planktonic groups averages more than 30% except for the $\pm 20\%$ case.
- The overall gain is not there much when the uncertainties are increased from $\pm 40\%$ and $\pm 60\%$.
- When the ranges given in Table 11.3 (from Shannon 2001) are used, the reduction in uncertainty is notably greater than even for the $\pm 60\%$ case.

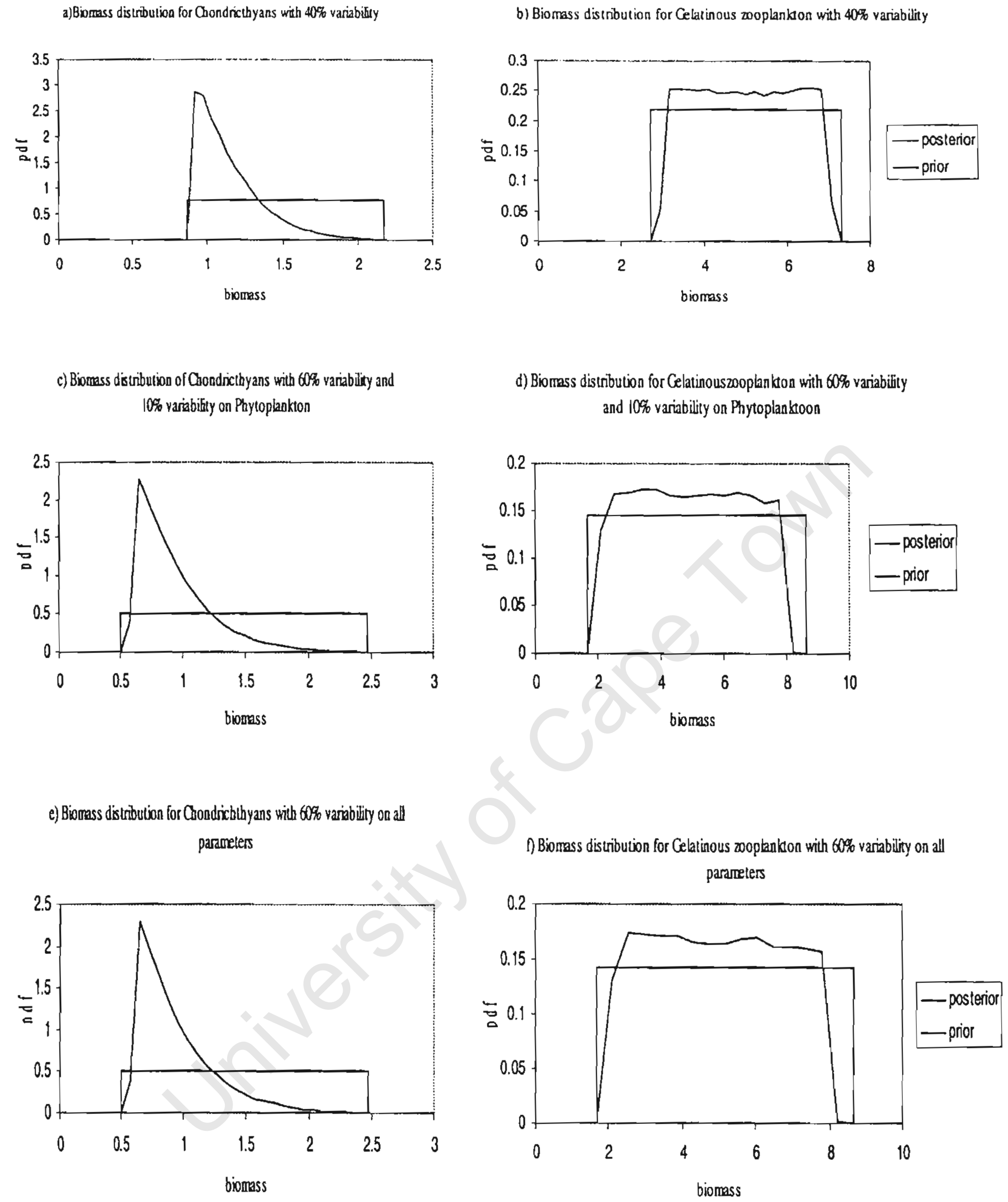
Fig. 14.1 compares prior and posterior probability density functions (pdf's) for biomass *(B)* for cases where there are both rather large and rather small updates of the priors for some of the scenarios. Figs 14.1 a, c and e (biomass for chondrichthyans) show considerable updating of the priors, with the peak of the pdf's towards the left which means the most probable values are less than the point estimates input. The Figs 14.1 b, d and f (biomass of gelatinous zooplankton) show the least updating: the posterior distributions do not indicate any more probable values with the input prior range.

Fig. 14.2 shows similar comparisons for the production:biomass *(P/B)* ratios for similar extreme instances of maximal and minimal updating. Note the indications in the left side plots that the *(P/B)* ratio for macrozooplankton is likely greater than the point estimate input.

Tables A.3-A.5 show the results for biomass *(B)* when certain inputs are treated as known exactly (fixed), rather than uncertain. These cases are directly compared to corresponding cases without such fixing (see also Figs 14.3-14.6). The results in broad terms are as follows:

- There are notably larger decreases in uncertainty for most groups when *P/B* is fixed for the ± 20% and ± 40% scenarios (Figs 14.3 and 14.4), but not for the ± 60% scenario (Fig. 14.5).
- Fixing the diet or improving the uncertainty on the phytoplankton biomass estimate has comparatively much less impact.

Table A.6 and Fig. 14.6 show similar results for production:biomass *(P/B)* ratios. Fixing the diet has relatively little impact on the extent of improvements that can be achieved.



a)Biomass distribution for Chondricthyans with 40% variability

b) Biomass distribution for Gelatinous zooplankton with 40% variability

c) Biomass distribution of Chondricthyans with 60% variability and 10% variability on Phytoplankton

d) Biomass distribution for Gelatinouszooplankton with 60% variability and 10% variability on Phytoplanktoon

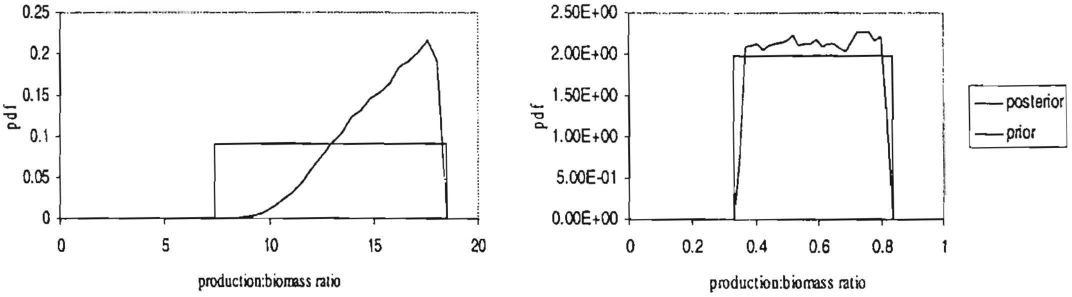
e) Biomass distribution for Chondrichthyans with 60% variability on all parameters

f) Biomass distribution for Gelatinous zooplankton with 60% variability on all parameters

Figure 14.1: Prior and posterior distributions for the biomasses of selected species (expressed in t/km^2). Figs a-b show results for priors over ±40% of input values, c-d for priors over ±60% with phytoplankton biomass uncertainty restricted to ±10% and e-f for priors over ±60% for all input values. Figs (a, c, f) on the LHS represent the biggest improvements in precision and (b,d,f) on the RHS represent cases where there is virtually no gain in precision.

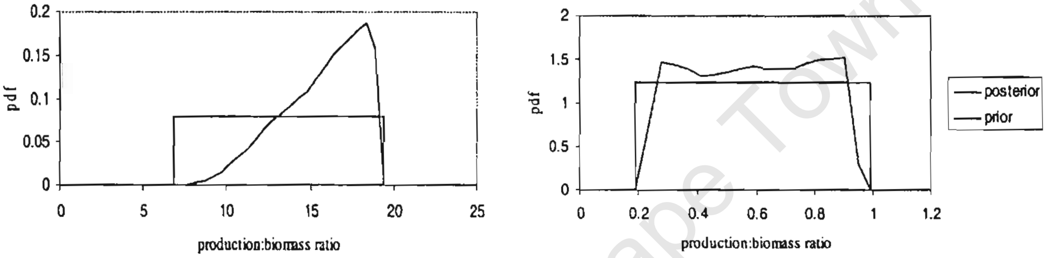
a) P:B distribution for Macrozooplankton with 40% variability

b) P:B distribution for Gelatinous zooplankton with 40% variability



c) P:B distribution of Macrozooplankton with 60% variability over input with 10% over Phytoplankton

d) P:B distribution for Gelatinous zooplankton with 60% variability over input and 10% variability on Phytoplankton



e) P:B distribution of Macrozooplankton with 60% variability over the input data

f) P:B distribution of Gelatinous zooplankton with 60% variability over the input data

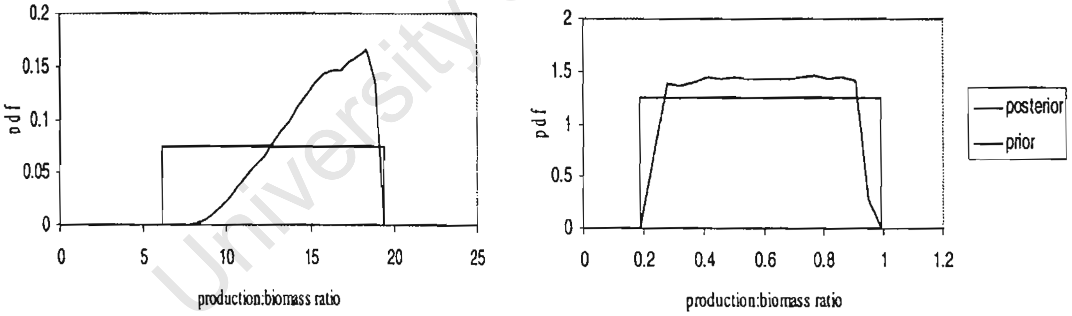


Figure 14.2: Prior and posterior distributions for the production:biomass ratios *P/B* (expressed as yr^{-1}) for selected species. Figs a-b show results for priors over ±40% of input values, c-d for priors over ±60% with phytoplankton biomass uncertainty restricted to ±10%, and e-f for priors over ±60% for all input values. Figs (a, c, f) on the LHS represent the biggest improvement in precision and (b,d,f) on the RHS represent cases where there is virtually no gain.

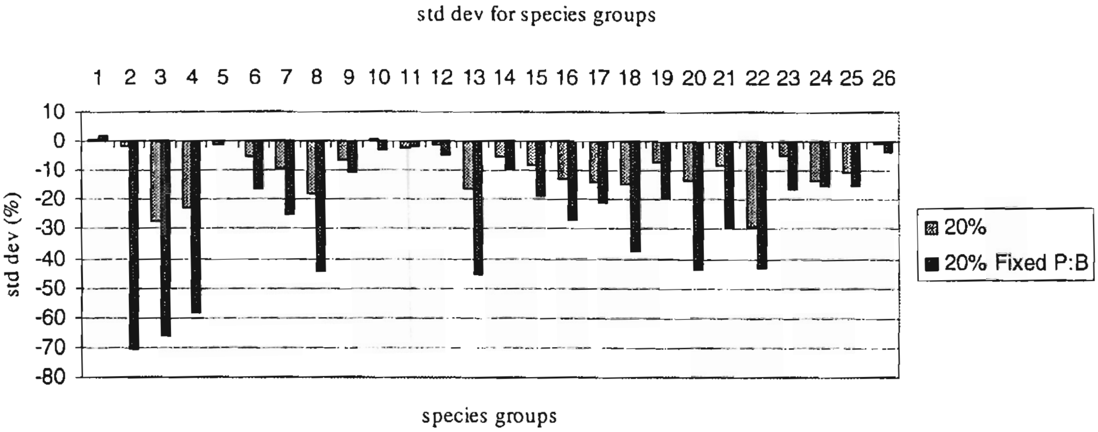


Figure 14.3: Improvements in the standard deviations of biomass *(B)* for 26 species or groups, comparing two cases when $\pm 20\%$ uncertainty is assumed for *B*, *P/B* and diet, and when *P/B* is fixed. The results show a larger decrease in uncertainty when *P/B* is fixed compared to the corresponding case when *P/B* is treated as uncertain.

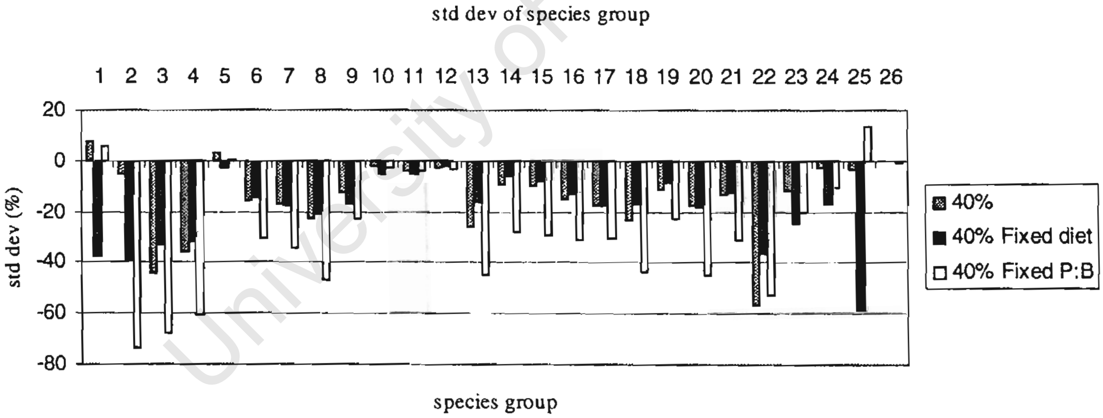


Figure 14.4: Improvements in the standard deviations of biomass *(B)* for 26 species or groups, comparing three cases when $\pm 40\%$ uncertainty is assumed for *B*, *P/B* and diet, when diet is fixed and when *P/B* is fixed. The results show a larger decrease in uncertainty when *P/B* is fixed compared to the two corresponding cases when *P/B* is treated as uncertain and when the diet is fixed. Fixing diet does not result in much reduction in uncertainty.

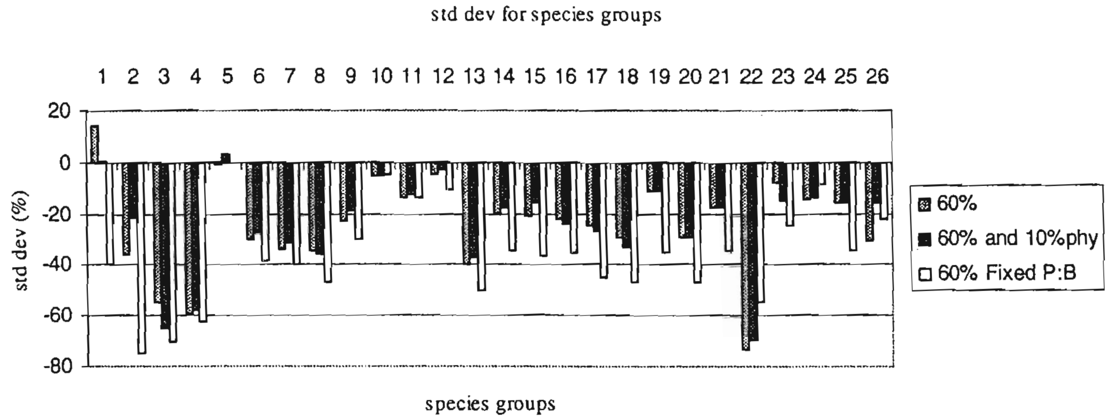


Figure 14.5: Improvements in the standard deviations of biomass *(B)* for the 26 species or groups, comparing three different cases: when ±60% uncertainty is assumed for *B*, *P/B* and diet, when uncertainty is restricted to ±10% for phytoplankton biomass, and when *P/B* fixed. The results show a larger decrease in uncertainty when *P/B* is fixed compared to the other two cases. Restricting uncertainty to ±10% for phytoplankton does not (substantially) change results for most groups.

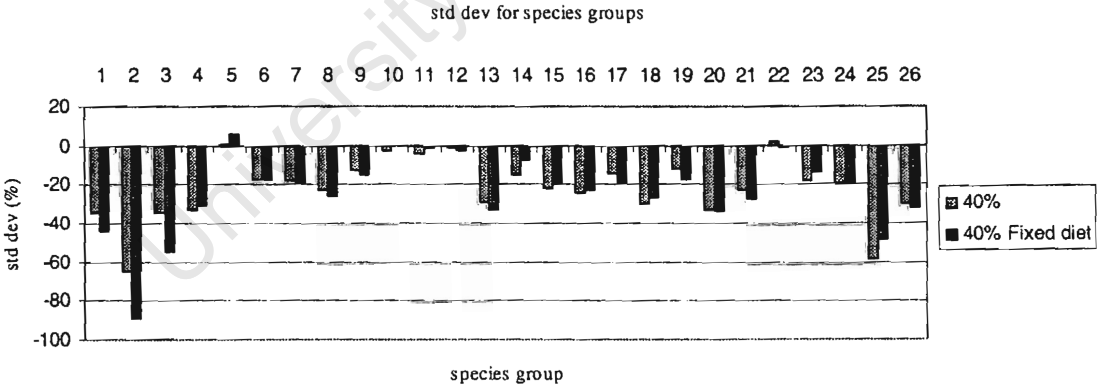


Figure 14.6: Improvements in the standard deviations of the production:biomass *(P/B)* ratios for 26 species or groups, comparing the two cases when ±40% uncertainty assumed for *B*, *P/B* and diet, and when diet is fixed. Fixing diet does not result in any substantial changes except for microzooplankton (group2) and perhaps sea birds (see group 25).

CHAPTER 15

CONCLUSIONS AND AREAS FOR FURTHER RESEARCH

15.1. Concluding remarks on the results

The key objective of this study has been to investigate the potential for the constraints associated with ECOPATH to improve knowledge about species biomass and productivity parameters in the southern Benguela (i.e. ECOPATH'S ability to "inform" about possible values for parameters being investigated). In an attempt to analyze the problem so as to gather further insights about possible parameter values, uncertainties were introduced about the available point estimates for the southern Benguela ecosystem as explained in section 12.4 of Chapter 12. Results (see Chapter 14) showed some cases in which these multi-species considerations do provide additional information about possible parameter estimates. These conclusions are reached by comparing output posterior distributions with input priors, and considering the decreases in standard deviations and credibility intervals as measures of reductions in uncertainty. In summary:

1. There is a general decrease in uncertainty for both biomasses *(B)* and production:biomass *(P/B)* ratios (cf. Fig. 9.5) in percentage terms. The level of improvement increases with increases in the extent of uncertainty input (see Tables A.1 and A.2). In other words when the space of the input priors is large enough, the ECOPATH constraints do lead to posterior distributions which reflect non-trivial improvements in uncertainty. However, if input

uncertainties are low, the ECOPATH constraints do not provide much by way of updating/improvement.

2. Inspection of differential improvement achieved if some inputs were known with greater certainty indicates that improved precision for inputs for *P/B* would be more valuable than improvements for diet composition.

15.2. Usefulness of the results

Some insights follow from these results for particular groups and species in the Southern Benguela ecosystem in general. The results from this kind of analysis may be used in conjunction with the results from other modelling approaches, including single species modelling and ecosystem modelling approaches.

1. For species or groups where there was scarcely any update of the priors, the absence of update suggests that ECOPATH and its constraints are unlikely to provide further insight, and hence direct measures need to be made to reduce uncertainty. The results suggest that reducing uncertainty in diet composition of the species groups will have less impact in reducing uncertainty than reducing uncertainty in P:B ratios. Thus ECOPATH provides an aid in pinpointing gaps in the present information where more focus is needed to establish better estimates (Christensen *at al.* 2004).
2. For cases in which updating of the priors did occur, for example chondrichthyans, inference became possible about raised biomass *(B)* or production: biomass ratio *(P/B)* values. Some independent verification using the single species approaches would be desirable. If the likely values indicated by the posterior distribution agree with those from such other modelling methods, more confidence can be associated with a claim that the constraints of ECOPATH do result in an improvement in knowledge about species abundance

and productivity. The verification could be achieved via an iterative process in which estimates from different modelling techniques are compared in order to better understand the abundance estimates (Christensen *at al*. 2004).

15.3. Areas for further work

The calculations in this paper have, almost without exception, assumed the same extent of input uncertainty for all species/ species groups in the ECOPATH model. These uncertainties need to be carefully re-evaluated on a species by species basis to provide better inputs for priors. The fact that estimates for some species are much better determined than those for others could result in differences to the conclusions from the work here.

APPENDIX A:

INVESTIGATION OF A RANGE IN UNCERTAINTY OVER THE ESTIMATES OF BIOMASS AND PRODUCTION:BIOMASS RATIOS

This Appendix reports results for the scenarios a)-d) set out in section 12.4 of Chapter 12. Tables A.1 and A.2 compare five scenarios in terms of relative changes from prior to posterior for the ±20%, ±40% and ±60% for cases for a), together with case d) and the uncertainty ranges in Shannon (2001). These two tables show results for biomass and for production:biomass ratios respectively.

The next three Tables A.3 to A.5 show results for biomass for variants of the ±20%, ±40% and ±60% cases respectively. Finally Table A.6 shows such results for the production:biomass ratios for the ±40% case.

Table A.1 Relative changes from the prior to posterior distributions of **biomass** ***(B)*** for five different widths of the uniform prior distributions.

	a) 20% variability on B, P/B and diet						b) 40% variability on B, P/B and diet						c) 60% variability on B, P/B and diet						d) 60% variability on B, P/B, diet and 10% variability Phytoplankton						e) Ranges given in Table 11.3 from Shannon (2001)					
			90% PI						90% PI						90% PI												90% PI			
	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1 Phytoplankton	2	0	-1	0	0	-1	-3	7	2	1	4	7	8	14	-3	2	2	10	0	1	0	0	-1	1	2	0	-1	-13	-34	-1
2 Microzooplankton	4	-2	-1	1	0	-5	3	-5	-4	0	-3	-8	19	-36	-40	2	-34	-65	15	-21	-27	0	-18	-39	-7	-63	-14	-25	-62	-60
3 Mesozooplankton	9	-27	-12	1	-27	-32	16	-44	-28	2	-44	-69	17	-55	-46	1	-52	-87	22	-65	-48	1	-69	-108	7	-74	-27	-1	-34	-75
4 Macrozooplankton	6	-23	-9	1	-20	-27	13	-36	-24	1	-34	-53	20	-59	-47	2	-52	-98	21	-58	-47	2	-63	-96	31	-40	-42	7	-62	-53
5 Gelatinous zooplankton	1	-1	-1	0	-2	-1	0	3	1	0	2	4	-3	0	-1	0	-1	1	0	3	0	0	0	3	-2	0	0	-7	-15	2
6 Anchovy	2	-5	-2	0	-3	-6	8	-16	-13	1	-14	-25	15	-30	-36	1	-29	-52	14	-28	-35	1	-26	-47	1	-5	-2	-20	-63	-6
7 Sardine	5	-9	-4	1	-7	-13	13	-17	-15	1	-16	-30	17	-34	-37	1	-31	-59	18	-31	-38	2	-31	-57	2	-6	-2	-20	-62	-8
8 Redeye	6	-18	-8	1	-17	-22	12	-23	-18	1	-20	-37	16	-34	-39	2	-33	-61	16	-36	-39	1	-34	-62	46	-14	-17	46	100	-43
9 Othersmallpel	3	-6	-2	0	-4	-8	10	-13	-11	1	-10	-22	15	-23	-30	1	-19	-42	16	-19	-28	1	-18	-38	5	-9	-24	-13	-52	-12
10 Chubmackerel	-1	1	0	0	0	2	-1	-2	-1	0	-2	-2	2	-5	-8	-1	-5	-7	6	-5	-7	1	-2	-11	-4	-1	-11	-7	-25	1
11 Juvenilehorse	0	-2	0	0	0	-2	7	-4	-4	1	-3	-10	12	-14	-21	1	-11	-25	10	-12	-19	0	-11	-22	6	-50	-35	-14	-74	-53
12 Adulthorse	-4	-1	1	0	0	1	-5	-3	1	-1	-1	0	-2	-5	-2	-1	-3	-3	-2	-3	-7	-1	-4	-2	7	-4	-25	-7	-43	-11
13 Mesopelagic	5	-16	-6	0	-15	-20	8	-26	-19	0	-25	-37	13	-40	-38	0	-36	-61	14	-37	-38	1	-32	-59	13	-74	-37	-13	-77	-76
14 Otherlargepel	0	-5	-1	-1	-4	-5	-1	-9	-5	-1	-6	-9	2	-20	-23	-1	-17	-25	3	-18	-22	-1	-16	-23	-3	-10	-23	-14	-53	-8
15 Cephalopods	-7	-8	1	-3	-7	-3	-12	-10	1	-3	-5	-1	-6	-21	-14	-4	-14	-16	-8	-16	-13	-2	-11	-12	-2	-23	-19	-9	-36	-22
16 SmallM.capens	4	-13	-5	0	-11	-15	4	-15	-11	0	-14	-20	10	-22	-29	0	-21	-35	10	-24	-31	0	-24	-39	16	-42	-34	11	-25	-52
17 LargeM.capens	-9	-14	1	-4	-11	-8	-24	-18	4	-9	-14	-1	-40	-25	4	-14	-18	3	-39	-27	4	-16	-22	2	-4	-6	-29	-21	-77	-4
18 SmallM.parad	-1	-15	-3	-1	-10	-14	-2	-23	-10	-2	-16	-23	2	-29	-27	-3	-25	-34	1	-33	-28	-3	-27	-37	12	-34	-33	2	-40	-42
19 LargeM.parad	-7	-7	1	-2	-5	-2	-13	-11	1	-4	-6	-2	-16	-11	-5	-4	-8	-1	-17	-11	-4	-3	-6	-1	-3	-2	-30	-20	-75	-1
20 Pelagicdemers	3	-14	-4	0	-11	-16	4	-17	-13	0	-14	-23	9	-29	-32	0	-26	-43	7	-30	-34	0	-27	-42	22	-83	-33	18	-9	-86
21 Benthicdemers	3	-8	-3	0	-7	-11	6	-13	-11	0	-12	-19	7	-18	-24	0	-15	-27	10	-18	-24	0	-15	-29	32	-70	-29	79	113	-79
22 Chondrichthyans	-13	-29	2	-10	-29	-21	-37	-56	5	-24	-49	-20	-77	-74	12	-48	-73	-8	-72	-70	11	-45	-66	-6	-19	-33	-10	-20	-47	-20
23 Seals	-3	-5	1	-2	-3	-3	-11	-12	0	-4	-7	-4	-5	-8	-4	-3	-6	-3	-14	-15	-1	-6	-10	-4	-3	1	-29	-20	-75	2
24 Cetaceans	6	-13	-4	0	-10	-17	-1	-2	-2	0	-1	-2	5	-14	-14	-2	-10	-19	5	-14	-15	-1	-9	-19	6	-7	-16	-6	-30	-11
25 Seabirds	-6	-10	1	-3	-8	-6	-21	-3	3	-2	0	8	-35	-16	6	-18	-23	7	-43	-16	9	-13	-14	10	2	-15	-31	-20	-78	-16
26 Macrobenthos	2	-1	-1	0	-1	-2	-7	0	0	-1	-2	3	3	-31	-27	-2	-22	-36	-10	-16	-10	-3	-10	-10	92	1	371	-21	236	-45
Averages																														
Planktonic and other	4	-9	-4	0	-8	-11	4	-12	-9	1	-13	-19	11	-28	-27	1	-27	-46	6	-26	-22	0	-23	-41	20	-29	48	-10	7	-39
Pelagics	2	-7	-2	0	-6	-8	4	-12	-8	0	-10	-17	9	-23	-25	0	-20	-35	9	-20	-25	0	-19	-33	7	-20	-20	-7	-39	-24
Demersals	-1	-12	-2	-1	-9	-11	-4	-16	-7	-2	-13	-15	-5	-22	-19	-3	-19	-23	-5	-24	-19	-4	-20	-24	13	-39	-31	11	-19	-44
Top predators	-4	-14	0	-4	-13	-12	-18	-18	2	-7	-14	-4	-28	-28	0	-18	-28	-6	-31	-29	1	-16	-25	-5	-4	-14	-22	-17	-57	-11
Overall average	0	-10	-2	-1	-8	-10	-1	-14	-7	-2	-12	-15	0	-25	-20	-3	-22	-30	-1	-24	-19	-3	-21	-29	10	-26	-7	-5	-25	-30

Table A.2: Relative changes from the prior to posterior distributions of **production:biomass ratios** ***(P/B)*** for five different widths of the uniform prior distributions.

		a) 20% variability on B, P/B and diet						b) 40% variability on B, P/B and diet						c) 60% variability on B, P/B and diet						d) 60% variability on B, P/B, diet and 10% variability Phytoplankto						e) Ranges given in Table 11.3 from Shannon (2001)					
				90%PI						90 % PI						90% PI						90%PI						90% PI			
		median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	2	5	1	1	3	4	24	-35	-25	2	-27	-46	1	-7	0	0	-3	-7	1	-7	0	0	-3	-8	1	-9	-2	-6	-18	-9
2	Microzooplankto	7	-48	-16	0	-48	-52	22	-65	-41	-2	-67	-71	18	-74	-129	-14	-75	-78	18	-29	56	-16	-293	-364	7	-55	-11	1	-59	-58
3	Mesozooplankton	10	-30	-13	1	-30	-36	21	-34	-29	1	-34	-44	29	-38	-91	2	-36	-51	29	-61	48	2	-57	-104	33	15	-41	9	-44	-14
4	Macrozooplankto	11	-28	-12	1	-28	-34	21	-33	-28	2	-31	-43	25	-47	-86	-6	-46	-56	25	-87	46	-7	-84	-127	2	-70	-31	-20	-76	-70
5	Gelatinous zoop	0	-2	0	0	0	-2	1	1	1	0	1	0	1	0	-2	0	-1	0	1	0	2	0	-1	0	2	0	-2	-7	-16	-1
6	Anchovy	5	-9	-3	0	-6	-13	13	-17	-15	1	-14	-25	20	-23	-52	1	-20	-34	20	-30	34	1	-26	-52	2	-8	-2	-20	-62	-9
7	Sardine	5	-10	-4	1	-8	-13	13	-18	-19	2	-18	-27	23	-23	-58	1	-22	-35	23	-29	37	1	-29	-54	3	-6	-2	-20	-62	-8
8	Redeye	9	-23	-9	1	-21	-28	16	-23	-22	2	-22	-32	25	-28	-74	2	-29	-41	26	-39	42	2	-40	-70	1	-96	6	-20	-60	-95
9	Othersmallpel	3	-4	-1	0	-1	-5	12	-13	-14	1	-13	-20	18	-16	-39	1	-15	-27	18	-20	28	1	-17	-38	5	-9	-24	-13	-53	-13
10	Chubmackerel	0	1	0	0	1	1	1	-3	-1	0	-1	-4	11	-5	-11	1	-4	-12	11	-5	10	1	-4	-14	0	-66	-30	-20	-75	-66
11	Juvenilehorse	2	-2	0	0	-1	-3	6	-4	-5	1	-3	-5	14	-11	-24	1	-9	-20	14	-12	19	1	-10	-25	0	21	-30	-20	-75	21
12	Adulthorse	0	2	0	0	-1	2	0	-1	1	0	0	-1	7	-4	-9	1	-3	-9	7	-5	8	1	-3	-10	-39	-49	43	47	-60	-15
13	Mesopelagic	9	-21	-10	1	-21	-27	19	-29	-24	2	-25	-39	28	-31	-76	2	-30	-44	28	-44	43	2	-42	-79	5	-97	-32	-19	-79	-97
14	Otherlargepel	4	-8	-3	0	-6	-11	16	-15	-16	2	-14	-24	23	-20	-52	3	-19	-33	23	-25	34	2	-23	-50	0	-52	-30	-20	-75	-52
15	Cephalopods	4	-11	-4	1	-8	-14	16	-22	-20	1	-19	-31	25	-26	-67	2	-26	-42	26	-39	40	2	-35	-71	1	-55	-25	-20	-66	-56
16	SmallM.capens	8	-15	-6	1	-13	-21	18	-24	-22	2	-22	-34	28	-24	-65	2	-25	-39	28	-32	39	2	-33	-63	2	-4	-30	-20	-76	-6
17	LargeM.capens	0	2	1	0	1	2	11	-15	-15	1	-14	-22	27	-30	-74	2	-29	-43	27	-43	42	2	-41	-76	-1	-1	-30	-20	-75	0
18	SmallM.parad	11	-27	-12	1	-26	-33	22	-30	-27	2	-30	-41	34	-33	-82	2	-32	-48	34	-60	45	2	-47	-91	3	-62	-30	-19	-76	-64
19	LargeM.parad	0	0	0	0	0	0	10	-12	-10	1	-9	-19	22	-23	-57	2	-22	-35	22	-30	36	2	-28	-55	0	0	-30	-20	-75	-1
20	Pelagicdemers	11	-31	-13	1	-30	-37	21	-33	-28	2	-31	-43	31	-37	-94	2	-37	-51	31	-60	49	2	-58	-104	5	-99	-23	-13	-58	-99
21	Benthicdemers	8	-19	-8	1	-17	-24	17	-23	-22	2	-21	-33	26	-27	-64	2	-25	-40	26	-36	39	2	-33	-66	5	-96	-23	-13	-51	-99
22	Chondrichthyans	-1	-1	0	0	-1	0	2	2	-3	0	-2	1	14	-18	-45	1	-17	-27	14	-22	31	1	-21	-37	-1	-32	-22	-13	-49	-32
23	Seals	3	-5	-1	0	-2	-7	15	-18	-15	2	-14	-27	23	-21	-51	2	-19	-34	23	-27	34	2	-24	-52	145	15	-35	191	313	55
24	Cetaceans	6	-12	-5	0	-10	-16	16	-20	-19	1	-18	-29	19	-11	-26	1	-9	-22	19	-12	21	1	-10	-29	5	-39	-25	-13	-53	-41
25	Seabirds	9	-40	-16	1	-40	-45	24	-58	-41	2	-58	-66	27	-47	-117	2	-47	-59	27	-87	54	2	-89	-142	8	-84	-40	-19	-95	-85
26	Macrobenthos	2	-7	-3	0	-7	-9	12	-30	-25	1	-29	-38	23	-37	-87	1	-36	-48	23	-58	46	1	-56	-94	2	-100	-23	-13	-51	-100
	Averages																														
	Planktonic and other	5	-18	-8	0	-18	-21	17	-33	-25	1	-31	-40	16	-34	-66	-3	-33	-40	15	-84	33	-3	-82	-116	9	-36	-18	-6	44	-42
	Pelagics	4	-8	-3	0	-7	-11	11	-15	-14	1	-13	-21	20	-19	-46	1	-18	-30	20	-25	30	1	-23	-46	-2	42	-13	-22	-67	-39
	Demersals	6	-15	-6	1	-14	-19	17	-23	-21	1	-21	-32	28	-29	-73	2	-28	-43	28	-42	42	2	-40	-76	3	-43	-23	-17	-68	-43
	Top predators	4	-14	-5	0	-13	-17	14	-24	-20	1	-23	-30	21	-24	-60	2	-23	-36	21	-37	35	2	-36	-65	40	-35	-39	37	29	100
	Overall average	5	-13	-5	0	-12	-16	14	-22	-19	1	-21	-30	21	-25	-59	1	-24	-36	21	-44	34	0	-43	-72	8	-40	-20	-8	47	-19

Table A.3: The relative changes in **biomass** ***(B)*** when 20% uncertainty is assumed for biomass *(B)* and diet, but the production:biomass ratios *(P/B)* are fixed at the original estimates, in contrast to 20% uncertainty for the biomasses, production:biomass ratios and diet .

		20% variability on B, P:B and diet						20% variability on B, diet but fixed P:B ratios					
				90% PI						90% PI			
		median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	2	0	-1	0	0	-1	6	2	-1	1	1	-2
2	Microzooplankton	4	-2	-1	1	0	-5	16	-71	-25	1	-71	-75
3	Mesozooplankton	9	-27	-12	1	-27	-32	12	-66	-22	0	-65	-70
4	Macrozooplankton	6	-23	-9	1	-20	-27	11	-58	-20	0	-56	-62
5	Gelatinous zooplakton	1	-1	-1	0	-2	-1	-2	0	1	0	1	1
6	Anchovy	2	-5	-2	0	-3	-6	0	-16	-6	-1	-17	-17
7	Sardine	6	-9	-4	1	-7	-13	5	-25	-11	1	-25	-29
8	Redeye	6	-18	-8	1	-17	-22	7	-44	-16	1	-42	-48
9	Othersmallpel	3	-6	-2	0	-4	-8	0	-10	-4	0	-11	-11
10	Chubmackerel	-1	1	0	0	0	2	-1	-3	0	-1	-2	-2
11	Juvenilehorse	0	-2	0	0	0	-2	-2	-2	0	-1	-1	-1
12	Adulthorse	-4	-1	1	0	0	1	-6	-5	1	-2	-3	0
13	Mesopelagic	5	-16	-6	0	-15	-20	7	-45	-16	0	-43	-49
14	Otherlargepel	0	-5	-1	-1	-4	-5	-5	-9	0	-2	-5	-6
15	Cephalopods	-7	-8	1	-3	-7	-3	-11	-19	1	-5	-14	-11
16	SmallM.capens	4	-13	-5	0	-11	-15	3	-27	-9	0	-22	-29
17	LargeM.capens	-9	-14	1	-4	-11	-8	-12	-21	2	-6	-17	-13
18	SmallM.parad	-1	-15	-3	-1	-10	-14	1	-37	-10	-3	-34	-38
19	LargeM.parad	-7	-7	1	-2	-5	-2	-11	-19	1	-6	-18	-12
20	Pelagicdemers	3	-14	-4	0	-11	-16	8	-44	-16	0	-42	-48
21	Benthicdemers	3	-8	-3	0	-7	-11	5	-29	-11	0	-28	-33
22	Chondrichthyans	-13	-29	2	-10	-29	-21	-13	-43	2	-14	-43	-35
23	Seals	-3	-5	1	-2	-3	-3	-9	-16	1	-4	-11	-10
24	Cetaceans	6	-13	-4	0	-10	-17	5	-15	-6	0	-13	-19
25	Seabirds	-6	-10	1	-3	-8	-6	7	-15	-2	1	-4	-19
26	Macrobenthos	2	-1	-1	0	-1	-2	2	-3	0	0	0	-5
	Averages												
	Planktonic and other	4	-9	-4	0	-8	-11	8	-33	-11	0	-32	-35
	Pelagics	2	-7	-2	0	-6	-8	1	-18	-6	-1	-17	-18
	Demersals	-1	-12	-2	-1	-9	-11	-1	-29	-7	-3	-27	-29
	Top predators	-4	-14	0	-4	-13	-12	-3	-22	-1	-4	-17	-21
	Overall average	0	-10	-2	-1	-8	-10	1	-25	-6	-2	-22	-25

Table A.4: The relative changes in **biomass *(B)*** when 40% uncertainty is assumed for biomasses *(B)*, and production:biomass ratios *(P/B)*, with diet fixed, and also such case where such uncertainty is over *(B)* and diet, but *(P/B)* ratios are fixed at their original estimates. Note that the case when 40% uncertainty is assumed over biomasses, production:biomass ratios and diet is also included for comparative purposes.

		40% variability of B,P:B ratio and diet						40% variability on B, P:B ratio but fixed diet						40% variabity on B, diet but fixed P:B ratio					
				90%PI						90%PI						90%PI			
		median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	-3	7	2	1	4	7	-16	-38	-6	-18	-38	-29	16	6	-1	1	1	-3
2	Microzooplankton	3	-5	-4	0	-3	-8	24	-39	-48	2	-39	-50	33	-73	-87	2	-73	-80
3	Mesozooplankton	16	-44	-28	2	-44	-69	6	-33	-31	-1	-30	-38	26	-68	-75	0	-66	-74
4	Macrozooplankton	13	-36	-24	1	-34	-53	17	-32	-35	1	-30	-40	22	-60	-67	1	-58	-67
5	Gelatinous zooplakton	0	3	1	0	2	4	0	-3	0	0	-1	-2	0	0	1	0	0	0
6	Anchovy	8	-16	-13	1	-14	-25	9	-15	-13	1	-10	-21	7	-31	-33	0	-29	-36
7	Sardine	13	-17	-15	1	-16	-30	13	-18	-20	1	-16	-26	14	-35	-39	1	-32	-43
8	Redeye	12	-23	-18	1	-20	-37	12	-21	-24	1	-20	-28	16	-47	-51	1	-44	-54
9	Othersmallpel	10	-13	-11	1	-10	-22	12	-17	-20	1	-16	-24	10	-23	-26	1	-21	-29
10	Chubmackerel	-1	-2	-1	0	-2	-2	2	-6	-2	0	-1	-7	-5	-2	1	-1	-1	2
11	Juvenilehorse	7	-4	-4	1	-3	-10	12	-6	-8	1	-5	-13	-1	-4	-2	0	-2	-5
12	Adulthorse	-5	-3	1	-1	-1	0	-8	-2	1	-1	-2	3	-13	-4	3	-3	-3	5
13	Mesopelagic	8	-26	-19	0	-25	-37	7	-16	-16	0	-14	-21	15	-45	-48	0	-42	-52
14	Otherlargepel	-1	-9	-5	-1	-6	-9	5	-6	-4	0	-4	-9	-2	-28	-23	-3	-27	-29
15	Cephalopods	-12	-10	1	-3	-5	-1	-13	-8	1	-3	-5	1	-10	-29	-14	-6	-24	-24
16	SmallM.capens	4	-15	-11	0	-14	-20	2	-13	-12	0	-11	-16	7	-31	-30	-1	-28	-36
17	LargeM.capens	-24	-18	4	-9	-14	-1	-17	-18	3	-10	-17	-5	-25	-30	4	-17	-29	-12
18	SmallM.parad	-2	-23	-10	-2	-16	-23	-2	-17	-11	-2	-14	-17	3	-44	-35	-5	-40	-47
19	LargeM.parad	-13	-11	1	-4	-6	-2	-12	-9	1	-3	-4	-1	-21	-23	0	-11	-21	-8
20	Pelagicdemers	4	-17	-13	0	-14	-23	7	-18	-15	-1	-15	-22	16	-45	-48	0	-42	-52
21	Benthicdemers	6	-13	-11	0	-12	-19	1	-12	-11	0	-10	-14	6	-31	-31	-1	-29	-36
22	Chondrichthyans	-37	-56	5	-24	-49	-20	-26	-36	5	-20	-34	-18	-31	-53	5	-30	-52	-35
23	Seals	-11	-12	0	-4	-7	-4	-15	-25	0	-11	-22	-14	-10	-21	-4	-7	-17	-14
24	Cetaceans	-1	-2	-2	0	-1	-2	6	-17	-13	-1	-14	-21	3	-11	-9	-1	-10	-13
25	Seabirds	-21	-3	3	-2	0	8	-27	-59	5	-35	-61	-44	-10	13	3	1	4	18
26	Macrobenthos	-7	0	0	-1	-2	3	-8	9	2	1	4	12	-9	-1	-3	0	-3	2
	Averages																		
	Planktonic and other	4	-12	-9	1	-13	-19	4	-22	-20	-3	-22	-24	15	-33	-39	1	-33	-37
	Pelagics	4	-12	-8	0	-10	-17	5	-11	-10	0	-9	-15	3	-25	-23	-1	-23	-27
	Demersals	-4	-16	-7	-2	-13	-15	-4	-14	-8	-3	-12	-13	-2	-34	-23	-6	-31	-32
	Top predators	-18	-18	2	-7	-14	-4	-16	-34	-1	-17	-33	-24	-12	-18	-1	-9	-19	-11
	Overall average	-1	-14	-7	-2	-12	-15	0	-18	-10	-4	-17	-18	2	-28	-23	-3	-26	-28

Table A.5: The relative changes in **biomass** *(B)* when 60% uncertainty is assumed for biomass *(B)* and diet but the production:biomass ratios *(P/B)* are fixed to their original estimates. A further similar case where the uncertainty in phytoplankton biomass is reduced to 10% is also shown. A further case is also included for comparative purposes.

		60% variability on B, P:B and diet						60% variability on B, P:B, diet but 10% Phytoplankton						60% variability on B and diet but fixed P:B					
				90%PI						90%PI						90%PI			
		median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	8	14	-3	2	2	10	0	1	0	0	-1	1	28	-40	-50	2	-39	-53
2	Microzooplankton	19	-36	-40	2	-34	-65	15	-21	-27	0	-18	-39	51	-75	-65	3	-74	-83
3	Mesozooplankton	17	-55	-46	1	-52	-87	22	-65	-48	1	-59	-108	41	-70	-62	0	-69	-79
4	Macrozooplankton	20	-59	-47	2	-52	-98	21	-58	-47	2	-53	-96	36	-63	-59	1	-60	-72
5	Gelatinous zooplakton	-3	0	-1	0	-1	1	0	3	0	0	0	3	0	0	-2	0	-1	0
6	Anchovy	15	-30	-36	1	-29	-52	14	-28	-35	1	-26	-47	16	-38	-47	0	-37	-47
7	Sardine	17	-34	-37	1	-31	-59	18	-31	-38	2	-31	-57	24	-40	-49	1	-39	-51
8	Redeye	18	-34	-39	2	-33	-61	18	-36	-39	1	-34	-62	27	-47	-53	2	-46	-58
9	Othersmallpel	15	-23	-30	1	-19	-42	16	-19	-28	1	-18	-38	17	-30	-42	1	-30	-40
10	Chubmackerel	2	-5	-8	-1	-5	-7	6	-5	-7	1	-2	-11	-3	-5	-10	0	-5	-4
11	Juvenilehorse	12	-14	-21	1	-11	-25	10	-12	-19	0	-11	-22	7	-14	-26	0	-15	-20
12	Adulthorse	-2	-5	-2	-1	-3	-3	-2	-3	-7	-1	-4	-2	-17	-10	-2	-5	-7	3
13	Mesopelagic	13	-40	-38	0	-36	-61	14	-37	-38	1	-32	-59	26	-50	-52	0	-47	-60
14	Otherlargepel	2	-20	-23	-1	-17	-25	3	-18	-22	-1	-16	-23	2	-35	-40	-3	-33	-39
15	Cephalopods	-6	-21	-14	-4	-14	-16	-8	-16	-13	-2	-11	-12	-4	-36	-35	-7	-32	-36
16	SmallM.capens	10	-22	-29	0	-21	-35	10	-24	-31	0	-24	-39	15	-35	-43	-1	-33	-44
17	LargeM.capens	-40	-25	4	-14	-18	3	-39	-27	4	-16	-22	2	-28	-45	-18	-24	-44	-29
18	SmallM.parad	2	-29	-27	-3	-26	-34	1	-33	-28	-3	-27	-37	11	-47	-46	-5	-42	-53
19	LargeM.parad	-16	-11	-5	-4	-8	-1	-17	-11	-4	-3	-6	-1	-18	-35	-26	-12	-33	-26
20	Pelagicdemers	9	-29	-32	0	-26	-43	7	-30	-34	0	-27	-42	25	-47	-51	0	-45	-58
21	Benthicdemers	7	-18	-24	0	-15	-27	10	-18	-24	0	-15	-29	10	-34	-41	-1	-31	-42
22	Chondrichthyans	-77	-74	12	-48	-73	-8	-72	-70	11	-45	-66	-8	-48	-55	13	-43	-57	-20
23	Seals	-5	-8	-4	-3	-6	-3	-14	-15	-1	-6	-10	-4	-21	-25	-8	-12	-21	-10
24	Cetaceans	5	-14	-14	-2	-10	-19	5	-14	-15	-1	-9	-19	10	-8	-17	0	-8	-15
25	Seabirds	-35	-16	6	-18	-23	7	-43	-16	9	-13	-14	10	-37	-34	10	-28	-36	-5
26	Macrobenthos	3	-31	-27	-2	-22	-36	-10	-16	-10	-3	-10	-10	12	-22	-39	2	-25	-33
	Averages																		
	Planktonic and other	11	-28	-27	1	-27	-46	8	-26	-22	0	-23	-41	28	-45	-46	1	-45	-53
	Pelagics	9	-23	-25	0	-20	-35	9	-20	-25	0	-19	-33	10	-30	-36	-1	-29	-35
	Demersals	-5	-22	-19	-3	-19	-23	-5	-24	-19	-4	-20	-24	3	-40	-38	-7	-38	-42
	Top predators	-28	-28	0	-18	-28	-6	-31	-29	1	-16	-25	-5	-24	-31	-1	-21	-30	-12
	Overall average	0	-25	-20	-3	-22	-30	-1	-24	-19	-3	-21	-29	7	-36	-33	-5	-35	-37

Table A.6: The relative changes in **production:biomass** ***(P/B)*** ratios when 40% uncertainty is assumed for biomass *(B)*, and production:biomass ratios *(P/B)*, and diet fixed to original estimates. Note that the case when 40% uncertainty is assumed over biomasses, production:biomass ratios and diet is also included for comparative purposes.

		40% variability on B, P:B and diet						40% variability on B, diet and fixed P:B					
				90%PI						90%PI			
		median	stddev	lower	upper	width	CV	median	stddev	lower	upper	width	CV
1	Phytoplankton	24	-35	-25	2	-27	-46	26	-44	-58	2	-47	-54
2	Microzooplankton	22	-65	-41	-2	-67	-71	0	-89	-52	-22	-89	-89
3	Mesozooplankton	21	-34	-29	1	-34	-44	25	-55	-65	2	-54	-64
4	Macrozooplankton	21	-33	-28	2	-31	-43	17	-31	-35	1	-29	-40
5	Gelatinous zooplakton	1	1	1	0	1	0	-1	6	1	1	2	7
6	Anchovy	13	-17	-15	1	-14	-25	16	-17	-20	1	-16	-26
7	Sardine	13	-18	-19	2	-18	-27	14	-19	-22	1	-17	-28
8	Redeye	16	-23	-22	2	-22	-32	18	-26	-32	2	-26	-36
9	Othersmallpel	12	-13	-14	1	-13	-20	12	-15	-13	1	-10	-23
10	Chubmackerel	1	-3	-1	0	-1	-4	1	0	-2	1	0	-2
11	Juvenilehorse	6	-4	-5	1	-3	-8	1	-1	-1	0	0	-1
12	Adulthorse	0	-1	1	0	0	-1	3	-3	-1	0	-1	-5
13	Mesopelagic	19	-29	-24	2	-25	-39	22	-33	-39	2	-31	-43
14	Otherlargepel	16	-15	-16	2	-14	-24	11	-7	-12	2	-8	-15
15	Cephalopods	16	-22	-20	1	-19	-31	17	-19	-22	1	-18	-29
16	SmallM.capens	18	-24	-22	2	-22	-34	17	-23	-27	1	-21	-32
17	LargeM.capens	11	-15	-15	1	-14	-22	8	-19	-18	0	-17	-25
18	SmallM.parad	22	-30	-27	2	-30	-41	22	-27	-33	2	-25	-38
19	LargeM.parad	10	-12	-10	1	-9	-19	8	-17	-14	0	-13	-22
20	Pelagicdemers	21	-33	-28	2	-31	-43	21	-34	-41	2	-33	-44
21	Benthicdemers	17	-23	-22	2	-21	-33	19	-28	-32	1	-26	-38
22	Chondrichthyans	2	2	-3	0	-2	1	3	-1	-1	0	-1	-3
23	Seals	15	-18	-16	2	-14	-27	13	-14	-15	1	-12	-22
24	Cetaceans	16	-20	-19	1	-18	-29	10	-19	-18	1	-15	-26
25	Seabirds	24	-58	-41	2	-58	-66	15	-48	-53	0	-47	-55
26	Macrobenthos	12	-30	-25	1	-29	-38	14	-32	-37	1	-32	-40
	Averages												
	Planktonic and other	17	-33	-25	1	-31	-40	14	-41	-41	-3	-41	-47
	Pelagics	11	-15	-14	1	-13	-21	12	-14	-16	1	-13	-21
	Demersals	17	-23	-21	1	-21	-32	16	-25	-27	1	-22	-33
	Top predators	14	-24	-20	1	-23	-30	10	-21	-22	0	-19	-26
	Overall average	14	-22	-19	1	-21	-30	13	-24	-25	0	-22	-31

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