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Predicting Weight Composition of Fish Diets: Converting Frequency of Occurrence of Prey to Relative Weight Composition

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Abstract: Diet compositions expressed in weight are essential to determine the trophic relationships in energetic terms between the compartments within a system. Data from stomachs were compiled from a number of sources (62102 stomachs), covering four broad areas such as the Northwest Atlantic, South Africa, Senegal and the Azores Islands in order to explore the empirical relationships between the frequency of occurrence, which is of limited use in a modelling context, and the preferred index, relative weight composition. These empirical relationships were found to be highly significant.

Keywords: Fish diets, relative weight composition, frequency of occurrence.

INTRODUCTION

The growing interest in ecosystem-based management as a complementary approach to traditional single-species management has emphasized the importance of the availability of diet composition data. One such approach is the use of multispecies or ecosystem models for measuring fishery impacts on marine ecosystems, which is dependent on information on the trophic relationships between the components of the system (Hollowed *et al.* 2000) [1] (Mace 2001) [2] (Christensen and Pauly 2004) [3] (Christensen and Walters 2004) [4]. Another approach concerns the development of ecosystem indicators such as trophic level, derived from data on diet composition, which has been proposed as a useful indicator of fisheries impacts on ecosystems (Pauly *et al.* 1998) [5] (Pauly *et al.* 1998) [6] (Pauly *et al.* 2001) [7] (Pauly *et al.* 2002) [8] (Stergiou *et al.* 2007) [9].

Studies describing diet composition and feeding habits of fish through the examination of stomach contents are fairly standard and literature on this subject is abundant. There is, however, a general lack of consistency in presenting the results, which reduces the number of studies suitable for specific and comparative analyses (Cortés 1997) [10]. This study focuses on one such index, the frequency of occurrence of prey in the diet, defined as the percentage of fish stomachs analysed containing a particular prey item irrespective of the amount. It gives an indication of specific food habits but no information whatsoever on the contribution to the diet in energetic terms. Data on frequency of occurrence is generally considered to be of no use in modelling studies, where the definition of diet in weight or energetic content is essential. This is particularly unfortunate when the only available information in a data-limited situation is expressed as frequency of occurrence (e.g. Longhurst 1957) [11].

The objective of this study was therefore to explore a possible empirical relationship between frequency of occurrence and relative weight of prey in diet composition or feeding ecology studies in order to predict the contribution in relative weight, when the latter is not available. The model is based mainly on diet data from the North Atlantic, but may be applied in other areas as a first approximation when there is a lack of information on number, volume or weight of prey in the diet.

MATERIALS AND METHODS

Diet composition data from 62,102 stomachs were compiled from a number of sources, covering four more or less broad areas: the Northwest Atlantic, South Africa, Senegal and the Azores Archipelago (Table **1**). Emphasis was placed on gathering studies that provided diet composition both in terms of relative weight composition and frequency of occurrence. The data sources were peer-reviewed papers, online datasets, grey literature, and dissertations. As definitions of diet indices can vary, it is appropriate to define the relevant indices used in this study:

- Relative weight composition (called r.weight in our model) is defined as the weight of a prey item divided by the total weight of prey items observed in a predator diet. Data presented as relative prey volume was assumed to be equivalent to relative prey weight (MacDonald and Green 1983) [30].
- Frequency of occurrence (called r.occur in our model) is defined as the number of stomachs containing a prey item divided by the total number of non-empty stomachs for a specific predator species, usually expressed as a percentage (%). Thus, the sum of prey occurrences is

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Table 1. Data Sources On Fish Diet Composition Used in the Present Study

Sampling Area	Sampling Site	No. Species	No. Stomachs Sampled	No. Observations	Reference
NW Atlantic		101	49811	2433	[33]
South Africa	South-western Cape coast	14	2081	66	[12]
South Africa	Algoa Bay	1	128	40	[13]
South Africa	Between Walvis Bay and Agulhas Bank	3	472	40	[14]
South Africa	KwaZulu-Natal, eastern and western Cape	1	271	40	[15]
South Africa	Tsitsikamma National Park	2	202	41	[16]
South Africa	South and West Cape coast	6	768	122	[17]
South Africa	West coast	2	4465	22	[18]
South Africa	South-eastern Cape coast	2	148	106	[19]
South Africa	Eastern and Western Cape	2	620	189	[20]
South Africa	Eastern Cape coast	1	92	34	[21]
South Africa	Agulhas bank	1	137	23	[22]
Senegal		24	1531	653	[23]
Azores		11	1376	425	[24,25] [26,27] [28,29]
Total		172	62102	4234	

usually higher than 100% (or 1) for each predator species.

This definition of frequency of occurrence is the most common definition, but some studies include empty stomachs in the calculation. Also, we have encountered several studies, where the sum of occurrences adds up to 100%, probably by re-scaling. These differences in definition are often not clearly stated and therefore a comparison of results from different studies should be handled with care.

DATA SOURCES

The main source of stomach data from the Northwest Atlantic was the Food Web Dynamics Program (FWDP) database, from the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Centre (NEFSC), provided by Dr. Rodney Rountree (http://www.fishecology.org), available for the period from 1973 to 1990. However, as stomach sampling protocol changed in 1981, the present study considers only the period from 1981 to 1990. Data is given as frequency of occurrence based on total number of stomachs, including empty, and mean prey volume. Thus, frequency of occurrence was re-calculated based on non-empty stomachs only (Table **1**).

Stomach data concerning South Africa were gathered from a number of publications on different species, which presented the results of stomach content analysis as frequency of occurrence and relative weight composition (Table **1**). All of the Senegalese data originated from the work published by Andriamirado and Caverivière (1989) [23]. Data concerning the Azores were from peer-reviewed papers and a thesis (Morato 2001) [26].

DATA PROCESSING AND ANALYSIS

Stomach content data were grouped according to categories such as: sampling area, predator habitat, feeding type, predator size group, and prey group (Table **2**). Sampling area refers to the four broad area described above. Predator habitat was adapted from FishBase 2000 (Froese and Pauly 2000) [31], but simplified to pelagic, benthopelagic and demersal categories. Most data sources indicated an average mean length or a range of lengths for each predator species, which were used to define three broad size classes (Small < 30 cm; 30 cm ≤ Medium < 60 cm; and Large ≥ 60 cm. If size data was not given, Fishbase 2000 was used to obtain an estimate of "Common length". Feeding types were defined on the basis of diet weight information, using the following criteria:

- Piscivore: fish constituted at least 75% of the diet.
- Benthivore: benthic prey constituted at least 75% of the diet.
- Herbivore: plants and macroalgae constituted at least 90 % of the diet.
- Omnivore: plants and macroalgae constituted at least 10 % of the diet.
- Planktivore: plankton constituted at least 75 % of the diet.

Table 2. Number of Observations According to the Defined Categories: Area, Habitat, Ps.Group (Predator Size Group), and Feeding Type

Area Ha	bitat	Ps. Group	Feeding						Grand Total
			benthivore	carnivore	herbivore	omnivore	piscivore	planktivore	
azores	benthopelagic	large					33		
		medium		87					
		small					54		
	demersal	large					54		
		medium	85						
		small		58			54		
azores Total			85	145			195		425
nw.atlantic	benthopelagic	large		191			1		
		medium	18	178			2		
		small		19			3	2	
	demersal	large	123	133			74		
		medium	211	510			249	8	
		small	109	351			58		
	pelagic	large		15			25		
		medium		92			8		
		small		5				48	
nw.atlantic Total			461	1494			420	58	2433
s.africa	benthopelagic	large		20					
		medium		25					
		small	16		2	12			
	demersal	large	180				51	21	
		medium	86	54			89	26	
		small	45	34		5	16	20	
	pelagic	medium					2		
		small		17	2				
s.africa Total			327	150	4	17	158	67	723
w.africa	benthopelagic	large	7	28			20		
		medium	49				8		
		small	15						
	demersal	large	46	68			51		
		medium	47	199			30		
		small	8				5		
	pelagic	large	15				22		
		small		35					
w.africa Total			187	330			136		653
Grand Total			1060	2119	4	17	909	125	4234

- Carnivore: others, diet consisted primarily of fish and cephalopods.

The level of identification of prey items varied depending on the data source, but it was generally detailed. In order to make statistical analysis feasible and more generally applicable results, the prey were grouped into very broad categories:

- Benthic crustaceans: shrimps, crabs, lobsters, etc.

- Benthic invertebrates: not included elsewhere, for example Anthozoa, Ascidiacea, Bryozoa, etc.
- Cephalopods: squid, cuttlefish and octopus, including pelagic and demersal species.
- Echinoderms: starfish and brittle stars as well as Holothuroidea
- Fish: all fish species
- Molluscs: bivalves and gastropods primarily.
- Zooplankton: copepods, euphausiids, mysids, etc., as well as fish and crustacean larvae and eggs
- Plants: macroalgae and various plants, which were often not specified
- Worms: polychaetes primarily.

Apart from the above-mentioned groups, a phytoplankton group and a miscellaneous group that consisted of unidentifiable prey or detritus material were also defined. Observations of parasite occurrences in the stomachs were classified as miscellaneous and this group was excluded from the statistical analysis. Only prey items that contributed with at least 0.001 % in relative weight of the predators' diet were included in the analysis. The zero-values thus eliminated from the analysis corresponded to 3.3% of total number of observations (144 obs).

The data was log-transformed and modelled using Generalized Linear Models, which allows for the possibility to include factors (R software used) (Dalgaard 2002) [32]. The factors included correspond to the categories defined above: area, predator habitat, feeding type, predator size group, and prey group.

RESULTS

A simple regression of the r.weight ~ r.occur relationship was highly significant explaining 68% of the variation in the data. On the other hand, the model that included all factors

Table 3. Results of Model Variance Reduction Expressed in Adjusted R^2 (Adjusted on Degrees on Freedom) for the r.weight ~ r.occur Relationship. The Model Chosen for Subsequent Prediction is Highlighted and Refers to r.weight (log) as a Function of r.occur (log) Including the Effects of Prey Type on the Slope and Intercept of the Regression Line

Factors Included	F Statistic	df	Adj.R^2	p Value
prey + feeding + habitat + area + ps.group	537.7	4211	0.736	0.000
prey + feeding + habitat + area	581.0	4213	0.733	0.000
prey + feeding + habitat	667.2	4216	0.728	0.000
prey + feeding	755.0	4218	0.728	0.000
prey (+interaction)	***585.1***	***4214***	***0.724***	***0.000***
prey	1095.0	4223	0.721	0.000
none	8996.0	4232	0.680	0.000

added only 6% to the variation explained (adjusted R^2= 0.736) (Table **3**). The small increase in the variation explained showed that many of the included factors had limited explanatory power. The factor prey type was clearly important, resulting in a 4% increase in explanatory power, but all other factors could be eliminated without serious loss (loss of 1.5% in explanatory power). Including an interaction term (the effect on the slope of the regression line) did not result in a clear improvement, but was maintained in the model because of its highly significant effect (Table **4**).

Not surprisingly, the effect of the various prey types was of particular importance in the model (Table **4**; Fig. **1**). This

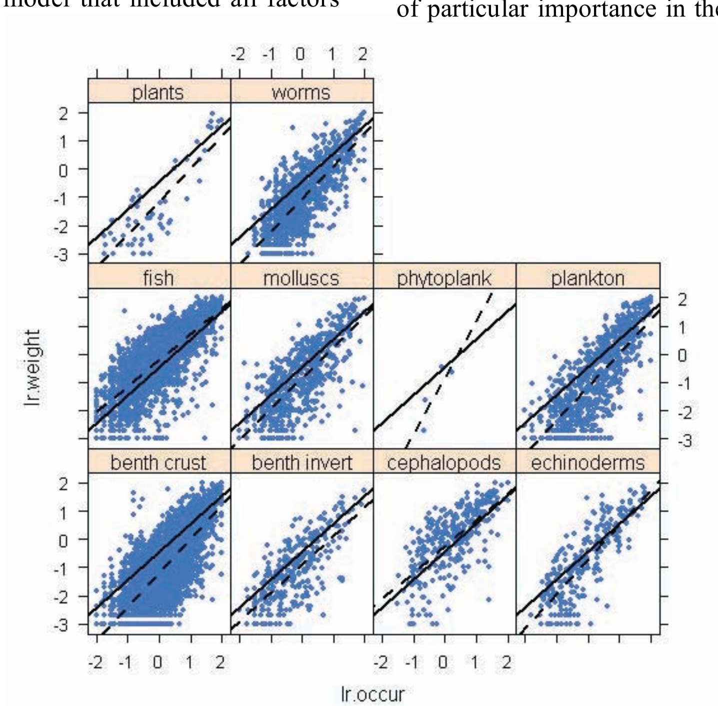


Fig. (1). Plot of r.weight as a function of r.occur considering the effects of prey categories. The reference line (bold) corresponds to a simple regression without the effects of prey, while the broken line is an independent regression of the observations (not to be confused with the equations given in Table **5**).

Table 4. Regression Coefficients for the r.weight ~ r.occur Relationship, which is a Linear Model with the Following General form: *(lr.weight) = a(intercept) + b(lr.occur) +* c_i*(prey) +* i_i*(lr.occur:prey);* where lr.weight is the Log-Transformed Relative Weight, lr.occur is the log-Transformed Frequency of Occurrence, a the Intercept, b the Slope, c_i the Coefficients of the factor term Depending on prey type (Additive Term on the Intercept), and i_i Refers to the Interaction Term Depending on Prey Type (Additive Term on the Slope). 95% Confidence Band Calculated as: 2.064*std. Error / Estimate

Coefficients	Estimate	Std. Error	Conf. Band	t Value	Pr(>|t|)
(Intercept)	-0.654	0.018	5.6%	-36.914	0.000
lr.occur	1.051	0.019	3.7%	55.080	0.000
prey_benth invert	-0.106	0.054	105.2%	-1.961	0.050
prey_cephalopods	0.376	0.047	25.7%	8.031	0.000
prey_echinoderms	0.110	0.059	109.7%	1.881	0.060
prey_fish	0.487	0.023	9.9%	20.898	0.000
prey_molluscs	0.038	0.037	200.5%	1.029	0.303
prey_phytoplank	-0.058	0.378	1342.8%	-0.154	0.878
prey_plankton	-0.023	0.039	351.1%	-0.588	0.557
prey_plants	-0.026	0.103	826.2%	-0.250	0.803
prey_worms	-0.055	0.055	206.9%	-0.998	0.318
lr.occur:prey_benth invert	-0.037	0.057	317.0%	-0.651	0.515
lr.occur:prey_cephalopods	-0.079	0.054	141.5%	-1.459	0.145
lr.occur:prey_echinoderms	0.153	0.060	80.8%	2.554	0.011
lr.occur:prey_fish	-0.102	0.025	50.1%	-4.118	0.000
lr.occur:prey_molluscs	-0.014	0.039	572.5%	-0.361	0.719
lr.occur:prey_phytoplank	0.209	0.959	946.8%	0.218	0.827
lr.occur:prey_plankton	0.089	0.039	91.6%	2.253	0.024
lr.occur:prey_plants	0.123	0.078	131.4%	1.571	0.116
lr.occur:prey_worms	0.049	0.054	225.0%	0.917	0.359

Residual standard error: 0.595 on 4214 degrees of freedom; Multiple R-Squared: 0.7251, Adjusted R-squared: 0.7239; F-statistic: 585.1 on 19 and 4214 DF, p-value: < 2.2e-16

was especially the case of fish as prey, where both of the additive terms on the intercept and slope were highly significantly ($p < 0.001$). A significant higher intercept was observed in the case of cephalopod and fish prey. For echinoderm and plankton prey the slope was significantly steeper.

Various conversion equations were defined on the basis of the regression model (Table **5**). Note however that the effects are not significant for specific prey types such as benthic invertebrates, molluscs, phytoplankton, plants and worms. For example, what looks like a clearly significant effect in the case of phytoplankton (Fig. **1**) is in fact not significant, probably due to the low number of observations (Table **4**). In such cases it would be acceptable to use the base regression line, which corresponds to benthic crustaceans (Table **5**; equation 1).

The distribution of model residual errors was slightly skewed, but the regression technique is considered to be a robust method, allowing slight deviations from the normal distribution (Appendix **1**). A long list of possible interactions were tested and found not to be significant or of limited value, but the results are not shown in order to simplify the presentation of the results.

DISCUSSION

It is generally difficult to standardize over different studies, so the approach used in the present study was to adopt broad prey categories. A lot of information is lost in this process and prey categories may include organisms of very different characteristics, but the results can be made more generally applicable. Occurrences of prey items, contributing with less than 0.001% in weight (zero-values), were excluded from the analysis as well as prey identified as miscellaneous. The number of observations that were excluded corresponded to about 6% of the total (zero-values: 3%).

There are many sources of variation when considering the diet composition of fish, which can stem from ecological factors or sampling procedures. Possible effects of sampling

Table 5. Equations for Converting from Frequency of Occurrence to Relative Weight Estimates, Taking into Account Various Types of Prey. Based on the Coefficients of the GLM Model (Table 4)

	Prey Type	Conversion Equation
1	benthic crustaceans	*y = -0.654 + 1.051x*
2	benthic invertebrates	*y = (- 0.654 - 0.106) + (1.051 – 0.037) x*
3	cephalopods	*y = (- 0.654 + 0.376) + (1.051 – 0.079) x*
4	echinoderms	*y = (- 0.654 + 0.110) + (1.051 + 0.153) x*
5	fish	*y = (- 0.654 + 0.487) + (1.051 – 0.102) x*
6	molluscs	*y = (- 0.654 + 0. 038) + (1.051 – 0.014) x*
7	phytoplankton	*y = (- 0.654 - 0.058) + (1.051 + 0.209) x*
8	plankton	*y = (- 0.654 - 0.023) + (1.051 + 0.089) x*
9	plants	*y = (- 0.654 - 0.026) + (1.051 + 0.123) x*
10	worms	*y = (- 0.654 - 0.055) + (1.051 + 0.049) x*

were ignored as the source of information covered many studies, using various methodologies. On the other hand, the approach used to define categories is one way of attempting to identify possible effects of ecological factors such as area (i.e. ecosystem), predator habitat and size as well as feeding type. Surprisingly, all of these factors had limited explanatory power and could be ignored with minimal loss in variance reduction. Habitat was the only factor not found to be significant (at the 5% level), which was considered to be a result of the importance of prey, thus making the factor habitat redundant.

A simplified model was chosen for the r.weight ~ r.occur relationship, including the effect of prey on both the intercept and slope. This model was highly significant ($p < 0.001$) and explained 72 % of the variation in the data, which may be considered a surprising result when taking into account all the various sources of variation as explained above. Although this model could be improved by adding further factor terms, we consider the simplified model satisfactory for a combination of explanatory power and ease of application. The model states that, on average, more frequently occurring prey species constitute an increasing part of the diet in terms of relative weight. Note that we do not even attempt to estimate absolute weights on the basis of occurrence. Although the effect of area could be ignored for general purposes, this effect was highly significant ($p < 0.001$). This was observed as lower intercepts for Azores and Senegal, indicating generally lower relative weights compared to the Northwest Atlantic and South Africa. Considering the general variability of diet data, we would nevertheless recommend the use of the conversion equations to obtain a first preliminary estimate (Table **5**), if the only available data is frequency of occurrence.

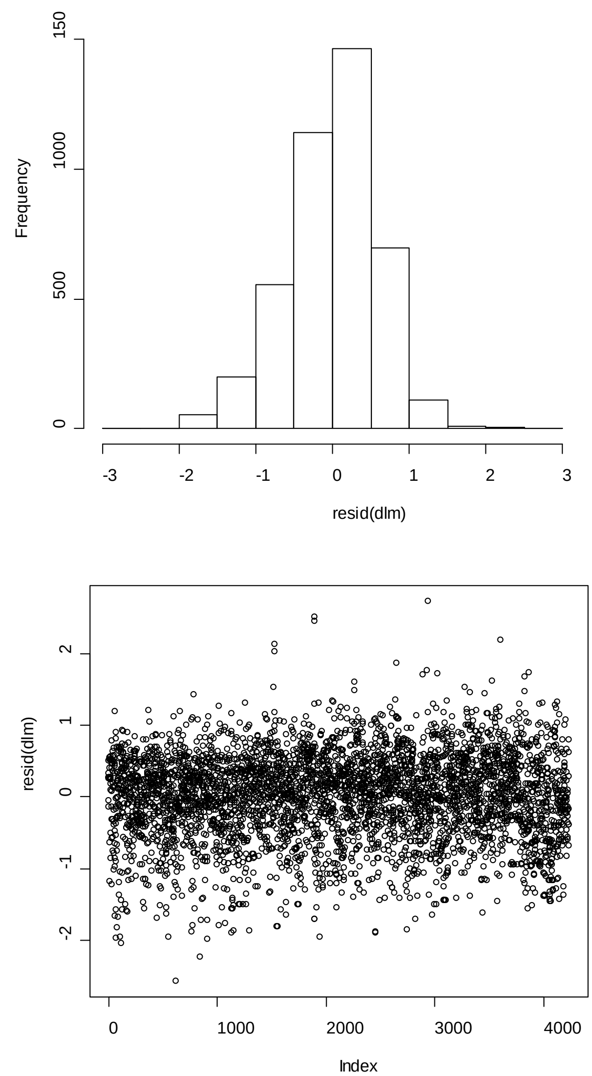
It should also be noted that the coefficients estimated by the model are relatively precise in case of prey such as benthic crustaceans (the base regression line), cephalopods, and fish (Table **4**: conf. band). This is however not the case for phytoplankton. Some examples have been prepared to illustrate this varying precision by including 95% confidence bands (Appendix **2**).

As far as we know, the present study is the first attempt to explore an empirical relationship between relative we ight composition and frequency of occurrence. Frequency of occurrence data has generally been considered to be of no use in quantifying trophic relationships as most recent modeling and indicator methods are built on biomass or energetic considerations. It was therefore surprising to observe in initial trials that this relationship could be modeled relatively well when considering relative and not absolute weights. This is of special relevance as many historical or earlier studies used the frequency of occurrence method to characterise fish diets and may be in some cases the only data available.

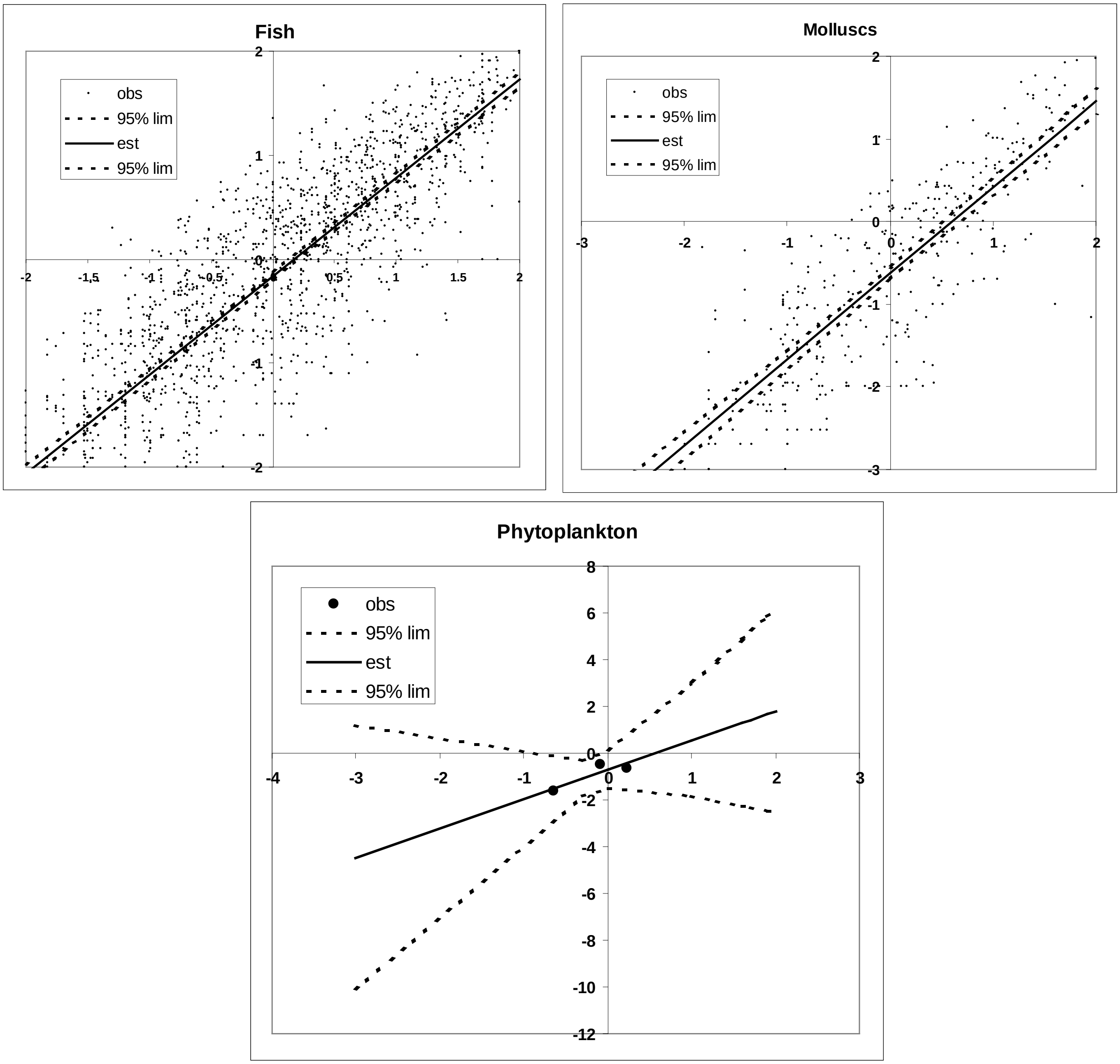
ACKNOWLEDGEMENTS

We would like to thank Ana Moreira (INIAP-IPIMAR) for assisting us in the processing of data and Dr. Rodney Rountree for his consent on the use of data from the FWDP programme. Furthermore, we thank Daniel Pauly and Deng Palomares for their encouraging words and the anonymous reviewers for improving this paper.

Appendix 1. Histogram and plot of model residuals, referring to the reduced model (Table 4)



Appendix 2. Plots of lr.weight ~ lr.occur Showing Model Estimates and 95% Confidence Band for Three Examples: Fish (High Precision), Molluscs (Medium Precision) and Phytoplankton (Low Precision)



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Received: February 28, 2008 Revised: February 23, 2009 Accepted: February 24, 2009