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Masters in Marine Biology

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Thesis developed in the University of Aberdeen:
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Abstract

In order to protect and sustainably manage fishery resources, it is essential to understand the temporal and spatial utilization of habitats of the target species. A Geographic Information System and length frequency analysis were used, in both fishery and survey data, to detect *Loligo forbesi* migration patterns from west to east coast of Scotland and inshore-offshore movements. Although the migration between west coast and North Sea is not evident, it is possible that veined squid performs an inshore movement in summer/autumn and offshore in winter/spring to complete their life cycle. Two distinct migratory behaviours between the two cohorts of Scottish veined squid is also a possibility, one cohort can be resident in inshore waters while the other migrates to offshore waters in winter and spring. The environmental reasons for such movements were examined using a generalized additive mixed model (GAMM) that suggested that distance to coast is the most important variable affecting size distribution in almost all seasons; however abundance distribution seems to be influenced with the same importance by sea surface temperature, depth and distance to coast. *L. forbesi* also revealed an optimal peak of abundance in waters at ~11^{o}C, 200m depth and 25miles far from coast.

Key words: *L. forbesi*, temporal and spatial distribution, GAMM, environmental variables.

Resumo

De modo a proteger e gerir de forma sustentável os recursos pesqueiros é essencial compreender como as espécies alvo utilizam os seus habitats temporal e espacialmente. Na lula riscada (*Loligo forbesi*) da Escócia isto é bastante importante uma vez que não existe qualquer medida de gestão da sua pesca, além do tamanho mínimo da malha das redes de arrasto. *L. forbesi*, encontra-se principalmente em águas costeiras, e nas águas escocesas apresenta duas coortes com dois períodos de desova e duas épocas de recrutamento. Diferentes estudos demonstraram que várias espécies de lulas fazem migrações de curta escala, de perto para longe da costa, e de grande escala, Este-Oeste ou Norte-Sul, e.g. a *L. forbesi* de Inglaterra. Estas movimentações poderão ser causadas por condições ambientais, nomeadamente pela temperatura e pela profundidade, uma vez que a abundância de várias espécies de lulas é influenciada por estas mesmas condições ambientais. Deste modo, os objectivos da presente tese são (1) verificar se *L. forbesi* faz migrações da costa Oeste para a costa Este da Escócia, no Inverno, para desovar e da costa Este para a Oeste, na Primavera, tal como sugerido por estudos anteriores; (2) detectar as eventuais migrações da *L. forbesi* da Escócia para zonas afastadas da costa e caso estes movimentos existam, verificar qual a sua relação com o ciclo de vida da espécie e; (3) verificar quais as razões ambientais que levam as lulas a migrar, dando ênfase à sua relação com a temperatura superficial do mar (SST), profundidade e distância à costa.

Para testar as hipóteses, foram utilizados dados de cerca de 20 anos da espécie *L. forbesi*, fornecidos pelo Fisheries Research Services, provenientes de desembarques comerciais e de navios de investigação. Estes foram primeiro utilizados num Sistema de Informação Geográfica (SIG) e em análises de frequência de comprimentos para verificar a existência de uma migração entre a costa Este e Oeste da Escócia. Estas análises demonstraram que a migração entre a costa Oeste e Este não é evidente, mas comportamentos migratórios diferentes entre coortes podem ocorrer, uma vez que alguns dos mapas de SIG exibem dois picos distintos de abundância em certos anos e meses. Outra explicação pode ser que a população de *L. forbesi* de Inglaterra, migre em certos anos mais para Norte que o habitual entrando no território escocês devido a condições ambientais mais favoráveis. Os mesmos dados foram utilizados para construir gráficos de abundância e frequência de comprimentos contra a distância à costa onde os arrastos foram feitos. Estes gráficos mostram que é possível que esta espécie migre para águas costeiras no Verão e Outono e para águas mais longínquas durante o Inverno e Primavera, com a finalidade de completar o seu ciclo de vida. A coorte que desova no Verão deverá fazê-lo em zonas costeiras assim como o seu recrutamento no Outono. Contudo, o local de desova da coorte de Inverno e as áreas de recrutamento na primavera não são claros. A hipótese de dois comportamentos migratórios distintos entre as duas coortes de *L. forbesi* da Escócia é também uma possibilidade: enquanto uma coorte é residente em águas costeiras a outra migra para longe da costa durante o Inverno e a Primavera, ou chega a estas águas longe da costa vindo de áreas ainda mais distantes como os Rockall Banks.

As razões ambientais para tais movimentos foram examinadas em R, com um modelo aditivo generalizado misto (GAMM), uma extensão do GAM, e com uma componente temporal (ano) como variável aleatória. Esta análise demonstrou que a distância à costa é a variável mais importante a afectar a distribuição por tamanhos, contudo, a distribuição da abundância parece ser influenciada igualmente pela SST, profundidade e distância à costa. A relação entre cada uma destas variáveis ambientais e o comprimento do manto da espécie em estudo varia consoante a estação do ano: e.g. no Inverno e Primavera quanto maior for o comprimento do manto mais próximo da costa se encontram as lulas, contudo, no Verão esta relação parece ser inversa. A influência destas variáveis na abundância é bastante uniforme ao longo dos diferentes meses: quanto menor a distância à costa maior será a abundância de lulas, até aos 200m de profundidade, quanto maior é a profundidade maior é a abundância e a abundância tem ainda um pico em águas com cerca de 10ºC. *L. forbesi* revelou, deste modo, ter um possível óptimo ambiental em águas escocesas com aproximadamente 10^{o}C, 200m de profundidade e próximo da costa.

Palavras-chave: *L. forbesi*, distribuição espacial e temporal, GAMM, condições ambientais.

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1. Introduction

In fisheries, it is essential to understand the temporal and spatial utilization of habitats (Arendt *et al.,* 2001), as well the life cycle (Collins *et al.,* 1997), of the target species in order to evaluate, protect and sustainably manage fishery resources.

In the veined squid *Loligo forbesi* (Teuthoidea, Cephalopoda) such knowledge is needed to underpin future management because, apart from a minimum legal mesh size of 40mm, imposed by European Union, and type of gear used, directed squid fisheries in UK are not subjected to management measures (Pierce *et al.,* 1998, Young *et al.,* 2006*a*). Although other cephalopods are caught in Scottish waters, *L. forbesi* is the most important, not only due its reliable market, but especially because it is an important by-catch product from Nephrops (Norway lobster) (Pierce *et al.,* 1994*a*, Young *et al.,* 2006*a*) and whitefish demersal trawl and seine net fisheries (Pierce and Boyle, 2003; Chen *et al.,* 2006). Increasingly it is also the target of small-scale directed fishing in Scotland (Young *et al.,* 2006*b*).

L. forbesi appears in the Northeast Atlantic coastal waters and offshore banks (Bellido *et al.,* 2001), between 20° and 60°N (Young *et al.*, 2006*b,* Chen *et al.,* 2006) and had a similar distribution range to *Loligo vulgaris,* however, nowadays in Scottish waters only *L. forbesi* is usually caught (Boyle and Pierce, 1994; Pierce *et al.,* 1998). In Scotland most landings of *Loligo* derive from three International Council for the Exploration of the Sea (ICES) fishery subdivisions: the northern North Sea (IVa), the West Coast of Scotland (VIa) and Rockall Bank (VIb) (Pierce and Boyle, 2003). Around October-December, the squid fishery in the two coastal fishery subdivisions (IVa and VIa) exhibits a clear annual peak (Bellido *et al.,* 2001, Chen *et al.,* 2006), as the breeding season approaches (Boyle *et al.,* 1995, Collins *et al.,* 1999).

L. forbesi is a semelparous species with a complex and short (approximately 1 year) life cycle (Collins *et al.,* 1995, Challier *et al.,* 2006). Several studies (Pierce *et al.,* 1995, Pierce *et al.,* 2005, Young *et al.,* 2006*a*) suggest that maturation and spawning display a clear winter peak in Scottish (UK) waters. Further studies regarding the life cycle of the veined squid refer to the presence of two breeding populations, the most important emerging in Winter and the other in Summer (Collins *et al.,* 1997, 1999; Zuur and Pierce, 2004; Pierce *et al.,* 2005), similar to what is seen in other squid species such as *Loligo gahi* from the Falkland Islands (Hatfield and Rodhouse, 1994; Hatfield and des Clers, 1998) and *Illex argentinus* from Argentina (Sacau *et al.,* 2005). The same studies suggest that these breeding populations, in Scottish and Irish waters, correspond to two distinct recruitment peaks, the main period, in late summer beginning of autumn, derived from the winter spawning (Collins *et al.,* 1997), and spring recruitment period from the summer breeder population. It is also possible that, despite the clear annual cycle, individual squid may live 18 months or longer, squids from winter breeders become the summer spawners of the following year, as discussed by Boyle *et al.* (1995).

Cephalopod populations are known to undertake migratory movements on all geographic scales (Boyle and Boletzky, 1996). Cephalopod species such as cuttlefish (Royer *et al.,* 2006) and squid species such as *L. gahi*, are known to move inshore to spawn and offshore to feed (Hatfield and Rodhouse, 1994; Arkhipkin *et al.,* 2004*a*). Hatfield & Cadrin (2001), after analysing length-frequency data from surveys, suggested that *Loligo pealeii* from the northeastern United States migrates seasonally with a movement to offshore waters during late autumn, and a return movement to inshore waters during spring and early summer. The same author also notes that when squid population migrates inshore, they are also moving southward and when offshore, northward.

According to Holme (1974), and confirmed later on by Sims *et al.* (2001) when studying the relationships between environmental conditions and abundance, *L. forbesi* also performs seasonal migrations in South-west England. This population hatches in the western English Channel during the winter (December-January) and migrates east towards southern North Sea. After a few months of rapid growth, they move back to the west area to spawn and die during the following December-January. Lordan and Casey (1999) reported that *L. forbesi* on the continental shelf edge and slope west of France, Ireland and in the Celtic Sea tend to spawn offshore.

For the Scottish *L. forbesi*, analysis of spatial patterns in fishery data, suggested that squid move from the West Coast of Scotland into the North Sea to spawn in winter (Waluda and Pierce, 1998). However, this proposed movement pattern has not yet been clearly investigated, since this is the only study on the subject, a small data set of five years was used and no statistical analysis was carried out.

Variability in local abundance (Robin and Denis, 1999; Bellido *et al.,* 2001, Waluda *et al.,* 2004), biological parameters (Robin and Deni,s 1999; Pecl *et al.,* 2004, Pierce *et al.,* 2005) and onset of migrations (Wang *et al.,* 2003, Arkhipkin *et al.,* 2004*b*) of cephalopods, including *L. forbesi*, have been previously shown to be affected by environmental conditions.

In the Falkland Islands, a simultaneous analysis of intra-annual distributions of water masses with the depth distribution of *L. gahi* was performed by Arkhipkin *et al.* (2004*a*). This study reveals that when spring warming starts at the end of October, squid from the spring spawning cohort begin to move into shallow waters to spawn, disappearing from the deeper areas. Therefore, when summer arrives, the new immature squids are found in the warmer waters of the inshore distribution area. As soon as they start to mature, in autumn, they move to shallow waters to the feeding grounds, changing areas with the autumn spawning cohort. Arkhipkin *et al.* (2004*a*) notes therefore, that even the coldest water living loliginid, follows the trends of other loliginids, being associated with the warmest possible water layers for its distribution.

According to Sims *et al.* (2001), *Loligo forbesi* movement in the English Channel is also temperature-dependent, migrating earlier in years when water temperatures are generally higher, and appears to be governed by climatic changes including the ones associated with the North Atlantic Oscillation (NAO). Waluda and Pierce (1998) and Pierce and Boyle (2003) used GIS and regression techniques, and Pierce *et al.* (2001) used GIS with generalized additive models (GAM) to investigate the relationship between Scottish *Loligo* abundance and environmental factors in fishery data. They demonstrated that squid abundance tend to be positively correlated with winter sea surface temperature (SST), with higher abundance in areas with higher temperature, and negatively correlated with summer SST. Pierce *et al.* (1998) found that the spatial pattern of catch rates for *Loligo* in trawl survey hauls in the North Sea in February could also be related to sea bottom salinity (SBT) and sea surface salinity (SSS).

Although these studies suggest that environmental conditions can be an important factor determining the movement patterns and trends in abundance of *L. forbesi*, relatively little is known about the details of its movement patterns in Scottish waters.

Migration movements have always been focus of interest in both terrestrial and marine environments. With the development of new technologies, such as Geographic Information Systems (GIS), visualization and linking of different types of data became easier, and hidden patterns and associations between them became clearer. Therefore, this in combination with statistical analysis methods facilitates improved studies in spatial-temporal trends (Pierce *et al.,* 2001).

Over the last decade ongoing development of statistical modeling tools has led to a growing sophistication in the methods used to analyze relationships between the distributions of species and their environment (Leathwick *et al.,* 2006). Methodology for nonlinear relationships, and for lack of independence among observations, is needed (Xiao *et al.,* 2004), since most statistical methods are based on the assumption that relationships between variables are linear, which is unrealistic for most ecological systems in nature. To solve this, the most common approach is transforming the data to linearise the relationships (Quinn and Keough, 2002), but this is not always successful.

In order to create a solution for this problem, Hastie and Tibshirani (1990) suggested generalised additive models (GAM), which are more flexible than linear models, but still interpreted since the link functions can be plotted to give a sense of the marginal relationship between the predictor and the response (Faraway, 2006). GAM allow for non-linear effects using smoothing models, therefore is basically a smoothing equivalent of generalised linear models (GLM) (McCullagh and Nelder, 1989) that allows the user to choose the amount of smoothing (degrees of freedom) for each explanatory variable (Wood, 2004). The advantage of these additive models is that the best transformation is determined simultaneously and without parametric assumptions regarding their form (Faraway, 2006). Although their use of non-parametric smoothing functions allows flexible description of complex species responses to the environment (Yee and Mitchell, 1991), their computational complexity makes awkward the generation of predictions for independent datasets such as in a GIS.

GAMs have increased in popularity in ecological fields and have been routinely applied to a combination of commercial and/or survey data together with geographic and environmental variables for understanding and predicting abundance, stock or species structure or distribution (Venables and Dichmont, 2004). Recent and detailed theoretical discussions appear in Schimek (2000) and Wood (2006), and recent examples of GAM analyses in ecology and fisheries can be found in Guisan *et al.* (2002), Xiao *et al.* (2004) and Zuur *et al.* (2007). Regarding cephalopods, Bellido *et al.* (2001) shows how GAMs can help to quantify the empirical spatial relationship found between its local abundance and environmental variables.

GAM, GLM or linear regression models can be applied to auto-correlated data, however the *p*-values of estimated parameters might be seriously under-estimated and the cross-validation (objective tool available to select the optimal degrees of freedom) might give misleading degrees of freedom for the smoothers (Ostrom, 1990; Bowman, 1997; Zuur *et al.,* 2007). For this reason, it is essential to include an auto-correlation structure for time series or spatial data. To solve this, GLM can be extended to a generalized linear mixed model (GLMM) that allow for auto-correlation in the residuals where the response is a random variable that follows an exponential family distribution (Faraway, 2006). A GAM therefore, can also be extended to a generalized additive mixed model (GAMM) that uses additive nonparametric functions to model covariate effects while accounting for overdispersion and correlation by adding random effects to the additive predictor (Lin and Zhang, 1999). This means that GAMM allows the application of smoothing methods while taking into account the spatial or temporal auto-correlation structure (Wood, 2006; Zuur *et al.,* 2007). In GAMM the response can be nonnormal from the exponential family of distributions; the error structure can allow for grouping and hierarchical arrangements in data and finally, is allowed for smooth transformations of the response (Faraway, 2006). The advantage of GAMMs, over GAMs, is in that the more complex stochastic structure allows treatment of autocorrelation and repeated measures situations (Wood, 2006).

Given this overview showing the lack of knowledge of movement patterns in veined squid, particularly in Scottish waters, and the power of new technologies and statistical approaches, the main objectives of the present work are (1) to confirm whether Scottish *Loligo forbesi* performs migration movements from West Coast to North Sea during winter time to spawn, and back again to West Coast to recruit in Autumn, as suggested by Waluda and Pierce (1998), (2) to establish the existence of seasonal inshore-offshore movements as documented in other *Loligo* species and, if these movements exist, to understand their relationship with the life-cycle, and (3) to determine the reasons for observed migratory movements, placing emphasis on the role of environmental conditions such as temperature and depth.

2. Material and Methods

This study used two types of data of Scottish (UK) *Loligo forbesi*. The first was commercial fisheries data of since 1980 until 2004, with exception of December 1996, collected mostly from registered demersal trawls. The second data source was from Scottish survey vessels on trawl catches from 1987 until 2004, the most frequently sampled months were August, December, February and March. All data used were collected by Fisheries Research Services (FRS) Marine Laboratory in Aberdeen (UK) and come from International Council for the Exploration of the Sea (ICES) subdivisions IVa and IVb (North Sea - NS) and VIa (West Coast of Scotland – WC) (Fig.1), since it is believed that *L. forbesi* is mostly a coastal species.

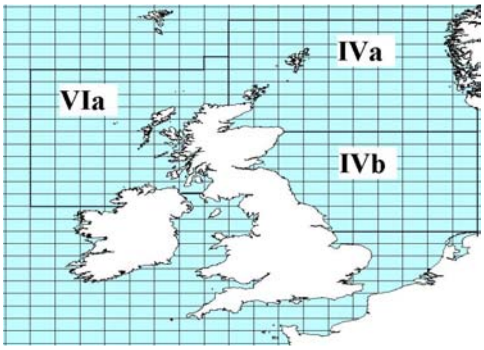


Fig. 1 – Map of International Council for the Exploration of the Sea (ICES) subdivisions for Scotland (UK) waters, IVa, b and VIa.

2.1. West Coast to North Sea migrations

2.1.a. As Zheng *et al.* (2001) had suggested and Waluda and Pierce (1998) had previously done for *Loligo* spp. in UK waters, in the present study, GIS was applied to visualize and describe the seasonal movements of *L. forbesi* abundance peaks along the Scottish coast. Monthly sums of commercial landings data (kg), of each ICES rectangle (i.e. the spatial resolution is 1° longitude and 0.5° latitude), were imported into a GIS system (ArcView 3.3 from ESRI) to create contour maps of the spatial distribution of squid abundance of each month and each year. The series were built from July to June of the following year because the most important recruitment season is thought to be between months July to November (Collins *et al.,* 1997) and these squid finally disappear from the fished population by June of the following year (Pierce *et al.,* 1994; Boyle *et al.,* 1995). These GIS abundance maps were displayed between 49^{o} and 63^{o}N.

Due to high commercial value, discarding of even small catches of *Loligo* is thought to be minimal (Young *et al.,* 2004) therefore landings can be assumed to accurately reflect catches. Catch per unit effort (CPUE) is frequently used as an abundance index (Pierce *et al.,* 1994*a*, 1998; Portela *et al.,* 2005; Wang *et al.,* 2007) however, this study used landings as abundance index rather than LPUE. Since 1998, FRS Marine Laboratory considers effort values of this fishery to be poorly reported due to a change in the recording system (Pierce GJ. *Pers Com.* 2007), but considers landings data to be reliable. In addition to this, a visual comparison between landings and LPUE values (calculated as hours of effort) was performed in this study with GIS. For years before 1997 this comparison revealed similar patterns in both indices, but years after 1997 that resemblance is not shown. Therefore we regard landings as an adequate abundance indicator and representative of the fishery (Fig. 2 and Appendix I).

As abundance and distribution of cephalopod stock may fluctuate widely from year to year because each year's stocks consist mainly of new recruits (Bellido *et al.,* 2001), contour maps where made without a standardized scale from one year to another.

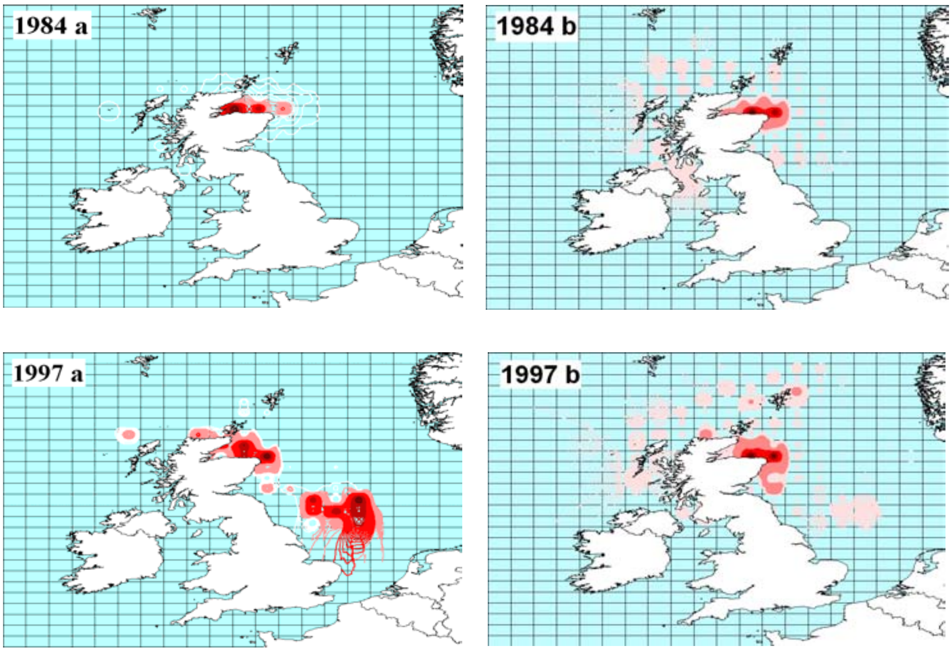


Fig. 2 – Maps showing *Loligo forbesi* abundance distribution in October of 1984 and 1997, in Scottish waters, achieved from CPUE (a) and landings (b). Squid abundance is characterized by a gradient colour scheme, from higher abundance in dark red to the lower abundance in light pink. (Landings in Kg and CPUE in Kg per hour of effort).

2.1.b. FRS Marine Laboratory performs regularly surveys in Scottish waters with the purpose to estimate young fish abundance. Although squid are not the target of these surveys, they are thought to be reliably recorded when present. The patchy occurrence of squid records in the survey data is thought to indicate a patchy distribution. The mantle length is one characteristic measured on board.

Length–frequency analysis has been used in several studies, either to establish geographic and temporal patterns (Hatfield and Cadrin, 2001; Arkhipkin *et al.,* 2006) or to resolve the presence of multiple cohorts and give indications of population growth in loliginid squid, including *L. forbesi* (Hatfield, 1996; Pierce *et al.,* 1994*b*; Collins *et al.,* 1995*b*, 1999). Therefore, to test the first hypothesis of the present work, in addition to the GIS method already described, data from Scottish surveys were used to produce length-frequency analysis. For that, and according to the months with at least one sample in all years in the respective area, a time series, with data from August from the North Sea (NS) – November/December from the West Coast (WC) – January/February (NS) – March (WC), was built for each year and this order. Series between 1993-1994 and 1995-1996 were not performed due to lack of sufficient data in all months. The mantle length was split into classes: animals between 1-4.5cm were considered to belong to length class 1, between 5-9.5cm to length class 2, 10-14cm to length class 3, 15-19cm to length class 4, 20-24.5cm to length class 5, 25-29cm to length class 6, 30-34cm to length class 7, 35-44cm to length class 8 and squids with 45-73cm were considered to belong to length class 9, in order to simplify the visual analysis.

These series were selected, as in the previous section, because the most important recruitment season is thought to be between months July and November (Collins *et al.,* 1997) and these squid disappear from the fished population by June of the following year (Pierce *et al.,* 1994*a*; Boyle *et al.,* 1995). In addition other reasons were accounted such as these were the months with at least one sample in all years, because the separation in years allowed a separation of different vessels/gears used in sampling, reducing the bias, and finally because in loliginid squid, size and maturity are positively related (Pierce *et al.,* 2005; Wood, 2000).

2.2. Inshore/Offshore migrations

Collins *et al.,* (1997, 1999), Zuur and Pierce (2004) and Pierce *et al.* (2005) suggested the existence of two breeding populations and two distinct recruitment peaks of *L. forbesi*, in Scottish and Irish waters. However is not clear from which cohort the two recruitment periods are derived. Therefore this section of the present work intended help to understand, not only the inshore and offshore movements, but also the connection between these movements and *L. forbesi* life cycle.

2.2.a. To explore the distribution patterns of *L. forbesi* in relation to shore, the distance of the centre of each ICES subdivision to the nearest coastal point (distance to coast.) was measured in GIS (ArcView 3.3). The nearest point to coast was measured instead of the nearest point to the mainland because it is thought that depth may have a positive influence on squid distribution and the many islands and Scandinavia peninsula, if neglected, could introduce an error.

Because in Scotland, each reported haul is associated with the approximate geographic coordinates where the haul was performed, was possible to combine this information with the measured distance from the centre of each ICES square, and determine the squid abundance distribution relative to coast. To investigate this distribution and eventual inshore/offshore movements, the sum of monthly landings (kg), from each ICES square, was plotted against the distance of the centre of each ICES square to the nearest coastal point, in which the haul was performed. As in GIS analysis section, the distribution series began in July due to the beginning of recruitment season (Collins *et al.,* 1997), and finished in June of the following year, when squid seem to disappear from fishing area (Pierce *et al.,* 1994*a*; Boyle *et al.,* 1995). These analyses were constructed for all the years in which data from commercial fisheries were available.

2.2.b. In other squid species, such as *L. pealeii* (Hatfield and Cadrin, 2001) length frequency analyses have been performed in survey data to study the connection between inshore and offshore movements, and between these movements and the life cycle. In the present study, a frequency analysis relating the distance of the haul to coast with *L. forbesi* length class, was therefore accomplished for each month and each year. The data came from survey vessels but only three classes, representative of small, medium and big squid, were examined, class 2 (5-9,5cm), 4 (15-19cm) and 6 (25-29cm), as size and maturity, in loliginid squid, are positively related (Pierce *et al.,* 2005; Wood, 2000). For that, the number of animals of each length class caught in a ICES square was plotted against the distance of the centre of that ICES square to the nearest coastal point. The series belonging to years 1987-90 and 1994-1996 were not built due to lack of consistent data throughout the months. As in length-frequency analysis, annual series were created with data from August (NS) - November/December (WC) – January/February (NS) – March (WC), because these were the months and areas with at least one sample in all years and because one of the hypothesis is that *L. forbesi* recruitment season begins in July, and finishes in June of the following year (Collins *et al.,* 1997).

2.3. Environmental analysis and statistics

To support and clarify the results from hypothesis 2, and to investigate whether there is a relationship between size and abundance distribution of *L. forbesi* in Scottish waters with environmental conditions (explanatory variables), a generalised additive model (GAM)

using an identity link function (i.e. Gaussian) was used as Hastie and Tibshirani (1990) and Zuur *et al.* (2007) suggested for non-linear data. However, the GAM approach does not take into account the auto-correlation of the different variables and also of these variables with years, due to the structure of data where years had to be combined. Additionally, the residuals dispersion showed great trend and the degrees of freedom of the model were extremely high which revealed that this approach was not appropriate (see Appendix II). GAM was therefore extended to a generalised additive mixed model (GAMM) as Lin and Zhang (1999) proposed for analysis of correlated data, where normally distributed random effects are used to account for correlation in the data.
To fit the model, the GAMM function available from R (version 2.4.0) mgcv library was used. The model selection was based on the absence of trend in residuals, and on identifying which explanatory variables had significant effects (significance is accepted only if $p<0.001$) with low degrees of freedom. The difference in the number of observations between data sets provided a reason to neglect the value of Akaike Information Criterion (AIC) for selection of the best fitted model, however was took into account if disproportionably high because can indicate the model is not well fitted to data.

SST was downloaded from the NCAR (National Center for Atmospheric Research, USA) web site, with a spatial resolution of 1^{o} longitude by 1^{o} latitude therefore had to be re-sampled to the spatial resolution of 1^{o} longitude by 0.5^{o} latitude, the same as the ICES statistical rectangles. This data are monthly average model results from remotely sensed data, survey temperature data, and sea ice distribution, (Reynolds and Smith, 1994). Sea depth data were downloaded from the website of the National Geographical Data Center, National Oceanic and Atmospheric Administration (NOAA, USA). The original data is gridded data with 5^{o} by 5^{o} resolution, therefore the mean depth of single ICES rectangle was calculated.

2.3.a. To model *Loligo forbesi* size distribution, the research survey data were divided into seasons: autumn/early winter (November and December), winter (January and February), spring (March and April) and summer (June to October). Each season had all years combined because available data are very variable from one year or season, to another; hence in some years observations are very few which could decrease the model strength. Therefore to minimize year impact on the model, this parameter was introduced in the equation as a random effect. Due to the complexity of the data, and subsequently difficulty in selecting the best model, two data sets were built for each season. The first incorporated each length class of each haul as a sample (response variable), and the second the average length of squid caught in each haul. A third option, each squid caught as an independent sample, was discarded because not only could introduce an error due to pseudo-replication (each squid is not a truly independent sample), but also because results showed similar patterns to those for the other two data sets, even not taking into account frequency of squid in each haul (see appendix I for more details) and as a final reason because the number of observations became to big to run in R which would lead to the introduction of one more difference in methods. Therefore for final result, a comparison between the models from each dataset was executed. GAMM was fitted to length (response variable, cm) with distance to coast of the centre of the ICES square sampled measured in miles, depth (m) and sea surface temperature (SST, ^{o}C) at which haul was performed, as explanatory variables.

2.3.b. As a final approach of this thesis, an attempt to find the relationships between squid abundance and environmental conditions was carried out in fishery data. However, one characteristic of *L. forbesi* fishery is that is mostly by-catch (Pierce *et al.,* 1994*a*; Pierce and Boyle, 2003; Chen *et al.,* 2006; Young *et al.,* 2006*a*) and therefore a large number of zero landings per haul is common. Due to the reasons explained above in this section, the approach to find links between environmental conditions and veined squid, was the application of a GAMM, however when modelling fishery data, residuals distribution was a problem revealing a very specific trend that indicated the model was not appropriate. Therefore, as data distributions with a high proportion of zero values are difficult to model in one step, a presence/absence approach was first considered and only afterwards the distribution of local abundance was modelled but only using presence data, as Maravelias (1999) and Bellido *et al.* (2001) suggested. To apply a GAMM in these presence data, landings values were natural log transformed, as the range of values was too wide, revealing some very extreme values that were interfering with residuals distribution, although all explanatory variables were kept once their transformation revealed no improvement to the model.

In both models, data from 1985 to 2004 were used because SST is only completely available since then, landings were used as response variable and distance to coast of the centre of the ICES square measured in miles, bathymetry depth (m) and SST (^{o}C) in which the haul was performed, as explanatory variables. In these GAMMs, year was also included as a random effect.

3. Results

3.1. West Coast to North Sea migrations

3.1.a. *Loligo forbesi* appears to be widely distributed around the Scottish coast. Commercial hauls were performed all around Scotland but the contour maps from fishery data reveal, in most of the studied years, a spatially restricted peak of abundance off North Scotland around May/June and an increase in abundance, with a spread in spatial distribution, towards the winter season. After this season, abundance begins to decrease and the spatial distribution also contracts. However, the spatial distribution does not show any clear and consistent pattern across all years in the time series, as we can see from the examples given in Fig. 3 and 4, representative of the years 1988-1989 and 2000-2001, respectively (see all annual GIS maps in Appendix III).

GIS maps reveal, in some years, a movement of the centre of abundance of *L. forbesi* from the West Coast to the North Sea in winter. However in other years, high squid abundance seems to appear mainly on the West Coast or mainly in the North Sea, or even shows a movement towards the West Coast in winter. *L. forbesi* seems to appear on the West Coast during spring and in the North Sea during summer in some years, but this is also not a consistent pattern, and again high squid abundance during both these seasons can appear on just one coast of Scotland. In some years, two distinct abundance peaks can also be seen in different areas. These maps are therefore geographic evidence against a consistent migration of veined squid migration from the West Coast of Scotland to the North Sea in wintertime and back again to West Coast in spring as previously hypothesised.

3.1.b. The length frequency analysis performed on survey data demonstrates that *L. forbesi* length distribution, for the same area and month, is very variable between years (Fig. 5). During August in the North Sea, there is a consistent dominance of small squid, especially length class 2; however, for the remaining seasons, squid size seems to show no clear pattern. In some years, the size classes in November-December are higher than in summer of the same year, and smaller than in January-February of the following year, while changing from West to East coast as expected. However this described pattern is not consistent in all years. In some other years, smaller squid in January-February than in November-December, or equivalent in size, can be observed along the different areas. The occurrence of relatively small squid in winter season, or even a mixture of sizes class is also apparent. When approaching spring in the West Coast, in several of the years for which data were available, squid seem to be smaller than in the previous season. During winter in North Sea, squid length classes are bigger than in spring on the west coast, in agreement with the present hypothesis; however there are exceptions. In some years, *L. forbesi* length class in spring is either the same as the previous season or bigger, which is not consistent with the present hypothesis. Length frequency analysis therefore does not provide evidence of veined squid migration from the West Coast of Scotland to the North Sea in wintertime, and back again to West Coast in spring (see Appendix IV).

3.2. Inshore/Offshore migrations

3.2.a. In Scottish waters, *L. forbesi* appears both inshore and offshore (Fig. 6). Between May and October, squid are caught mostly inshore since, according to the graphics of the distance to coast of squid abundance, only a very low abundance can occasionally be found in areas distant from the coast. However, between November and April of the following year, squid seem to be appearing both in inshore and offshore grounds. Therefore, around summer and autumn, as we can see from this analysis, *L. forbesi* tend to be close to shore, and around winter and spring time, they also appear far from the coast but never completely disappear from the inshore grounds. It is also visible that, in some years, the distance to coast of the main centre of squid abundance is slightly variable within months, in that abundance peaks can appear in, or disappear from, offshore grounds one month earlier or later.

Apart from this variation in timing, the appearance of *L. forbesi* in inshore and offshore grounds is clear and can be described as consistent. However, the movement to offshore grounds and from this area to inshore grounds is not as clear, since squid never really leave inshore areas (see Appendix V).

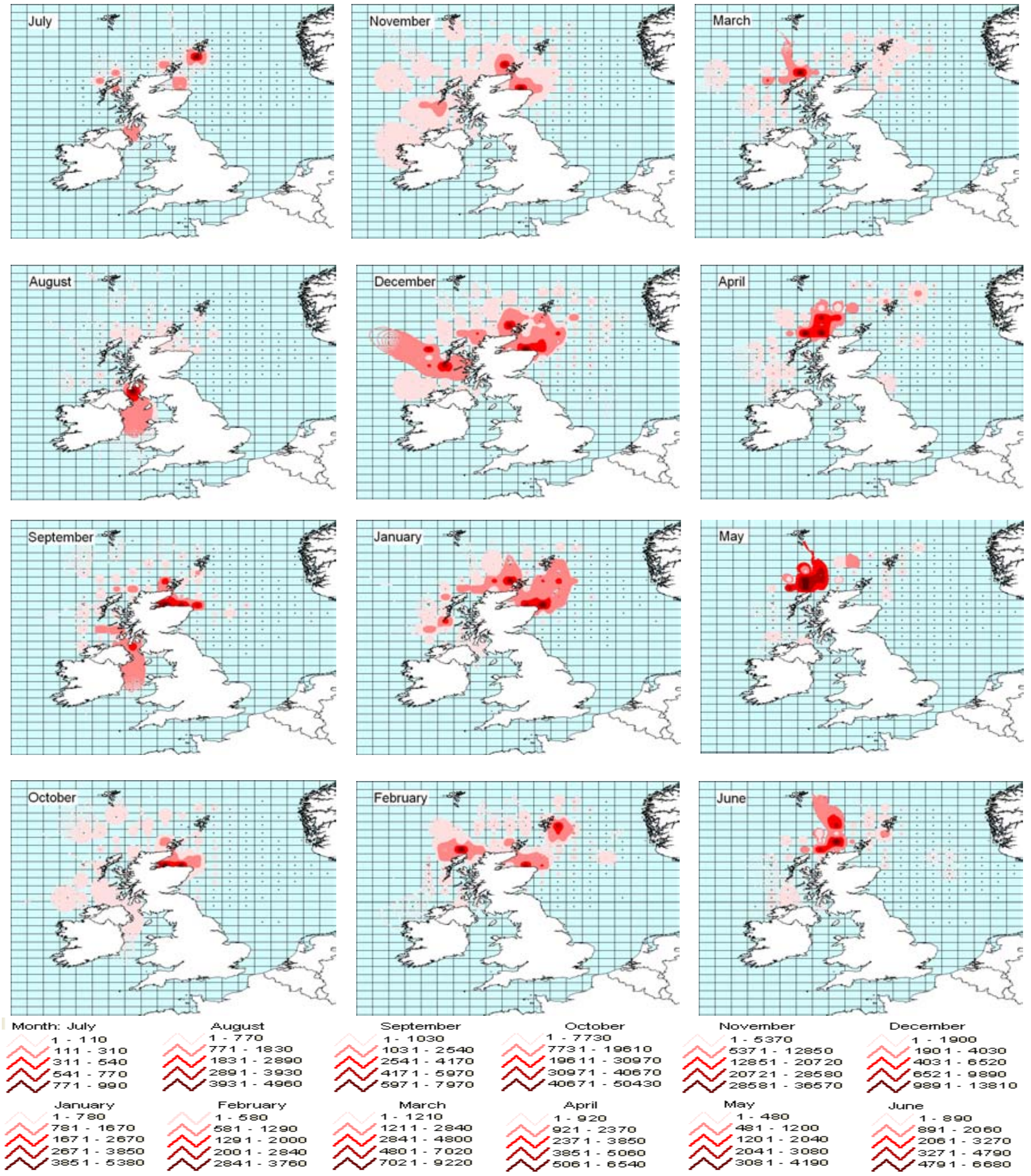


Fig. 3 – Contour maps of the annual distribution of *L. forbesi* abundance (Kg), from July of the year 1988 until June of the following year, 1989. Black dots represent the presence of haul(s) in the ICES square.

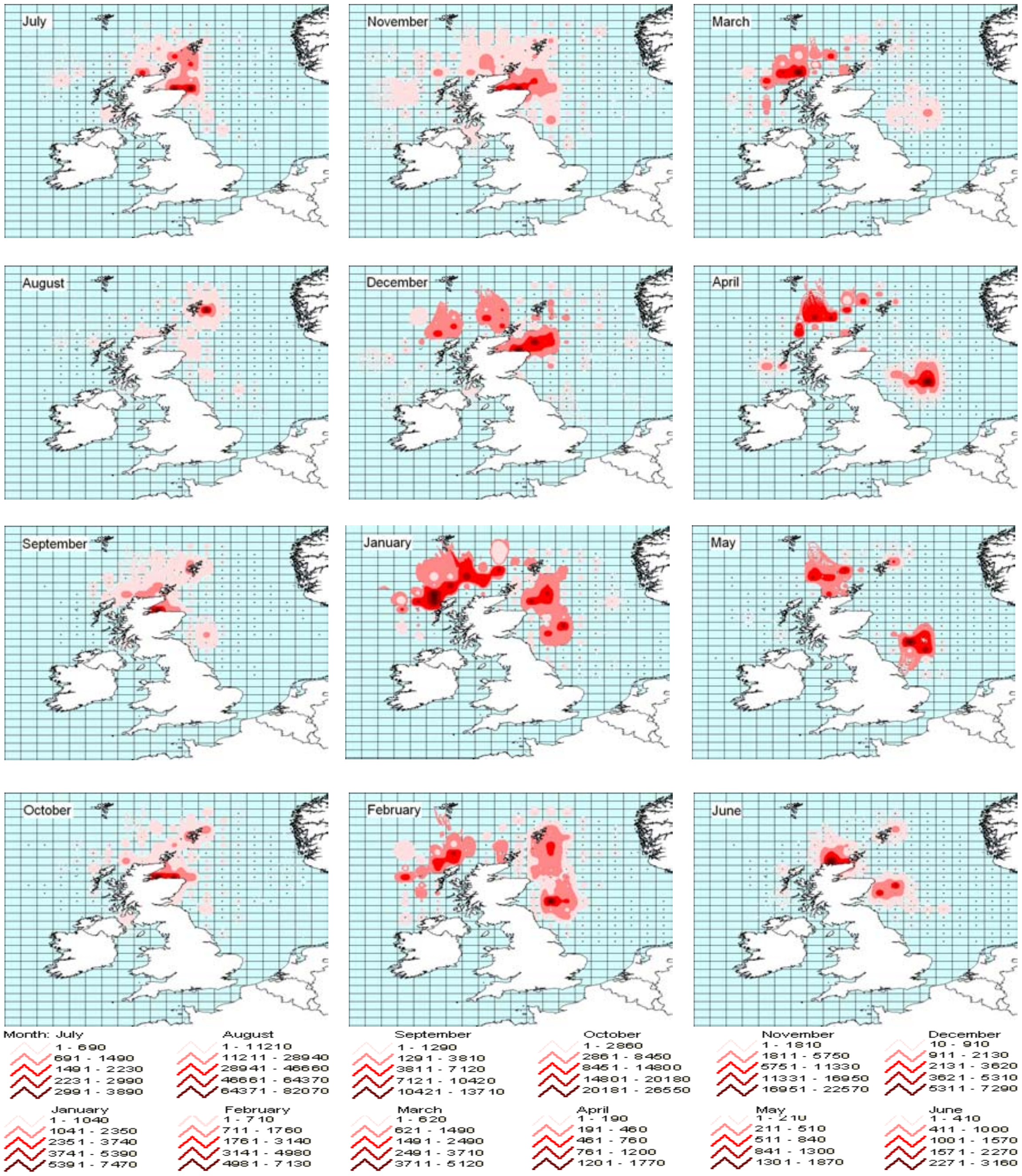


Fig. 4 – Contour maps of the annual distribution of *L. forbesi* abundance (Kg), from July of the year 2000 until June of the following year, 2001. Black dots represent the presence of haul(s) in the ICES square.

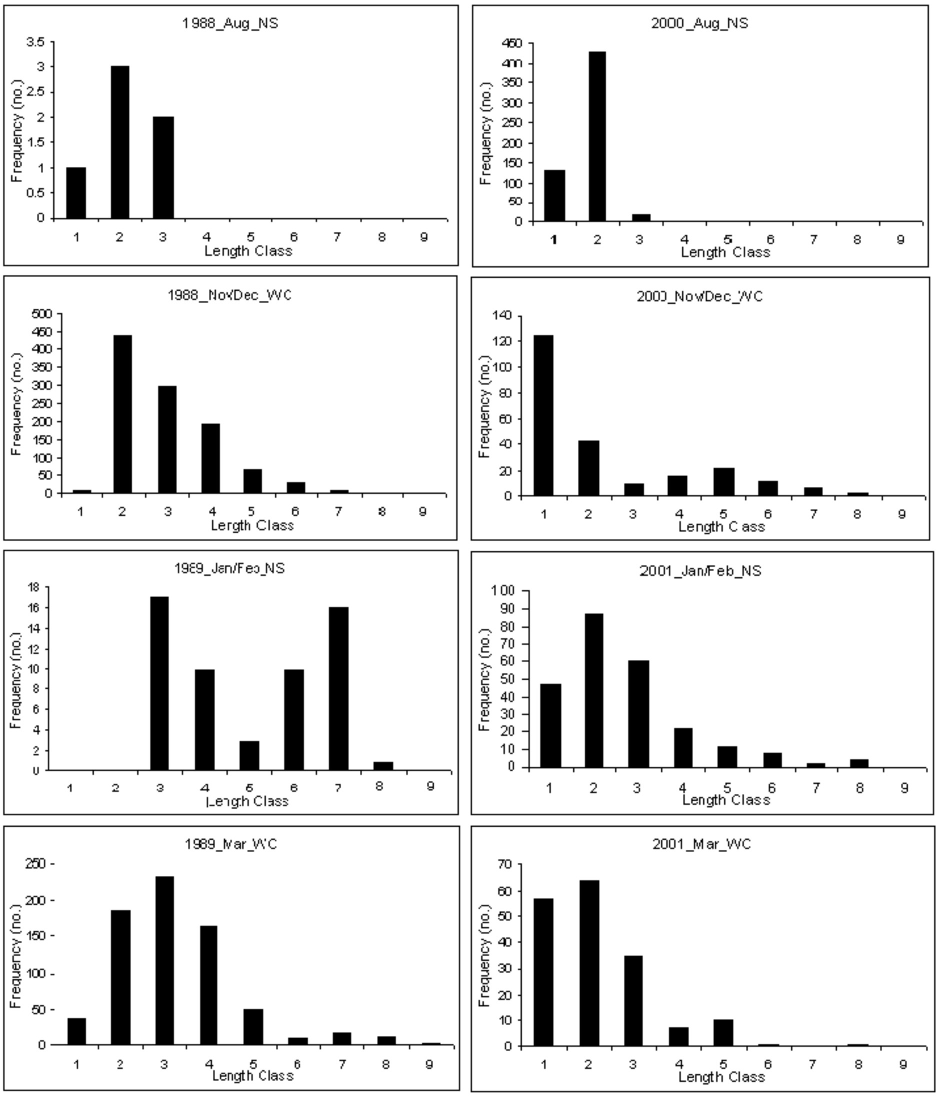


Fig. 5 – *L. forbesi* length-frequency distributions from 1988/1989 (left) and 2000/2001 (right). The series starts in August with data from the North Sea (NS) and November-December from the West Coast (WC), and continues to the following year in January-February with data from NS and March from WC. Animals of length class 1: 1-4.5cm; length class 2: 5-9.5cm; length class 3: 10-14cm; length class 4: 15-19cm; length class 5: 20-24.5cm; length class 6: 25-29cm; length class 7: 30-34cm; length class 8: 35-44cm; length class 9: 45-73cm.

3.2.b. *L. forbesi* from length classes 2, 4 and 6 seem to appear in both offshore and inshore grounds. The appearance of some squid in offshore grounds, between November and April, seem to be visible in the analysis of the distance of particular length classes from the coast (Fig. 7). Similar to what is seen in offshore areas, squids appearing exclusively in inshore grounds, around August, belong to all length classes studied in this section.

Small squid of length class 2 seems to appear close to the coast all year around, but in August and December they tend to aggregate only in inshore grounds. However, when spring season is approaching they seem to spread to offshore waters, while never disappearing from inshore waters. On the other hand, squid of length class 4 and 6 show a similar pattern, emerging both inshore and offshore all year, but with very low frequency in offshore waters in summer (August). In spring (March) squid seem to be closer to coast than in the previous season. This analysis of size in relation to distance from the coast revealed a spatial pattern throughout the year that is consistent with the above results of the distribution of abundance in relation to coast. These indicate some possible movements to offshore waters in winter and to inshore waters in spring, performed by both small and large squid (see Appendix VI).

3.3. Environmental analysis and statistics

3.3.a. Using a GAMM approach to analyse average squid size for both survey datasets, (A) treating the frequency of each length class present in each haul as a data point and (B) using the frequency of the average length from each haul respectively, revealed that the distance from coast where a haul is performed is the most significant explanatory variable in most seasons (see Tables I and II, respectively). The exception to this trend is the same in both models: during summer months, depth and SST seem to be the most significant variables, although the smoother for the effect of distance to coast is still significant for model A. When modelling A, all explanatory variables are significant but in B the same is only shown in spring (March-April). In autumn and winter the variable "distance to coast" is the most significant in both models. However when applying the GAMM to A, depth and temperature seem to have significant effects but when modelling B, these parameters seem to lose their effect on squid size distribution ($p>0.001$). In model B during autumn, even the effect of the smoother distance is very weak. During spring months, for both models A and B, effects of all explanatory variables are significant, but distance to coast is the most important variable in model B and depth is the most important in model A, although with very similar p values.

Regarding the degrees of freedom of the smoothers for these models, these vary between ~1 and ~8 in all seasons and for all explanatory variables. The smooth term "distance to coast" reveals the lowest values in almost all seasons (i.e. the effect is closest to being linear), but there is one exception to this pattern in autumn/early winter months, in which SST seem to have the lowest degrees of freedom. The dispersion of residuals was almost identical for both data sets (A and B) used in the present study and suggests that the GAMM approach is appropriate, since there is no apparent pattern in plots of standardised residuals against the fitted values for the models (Fig. 8).

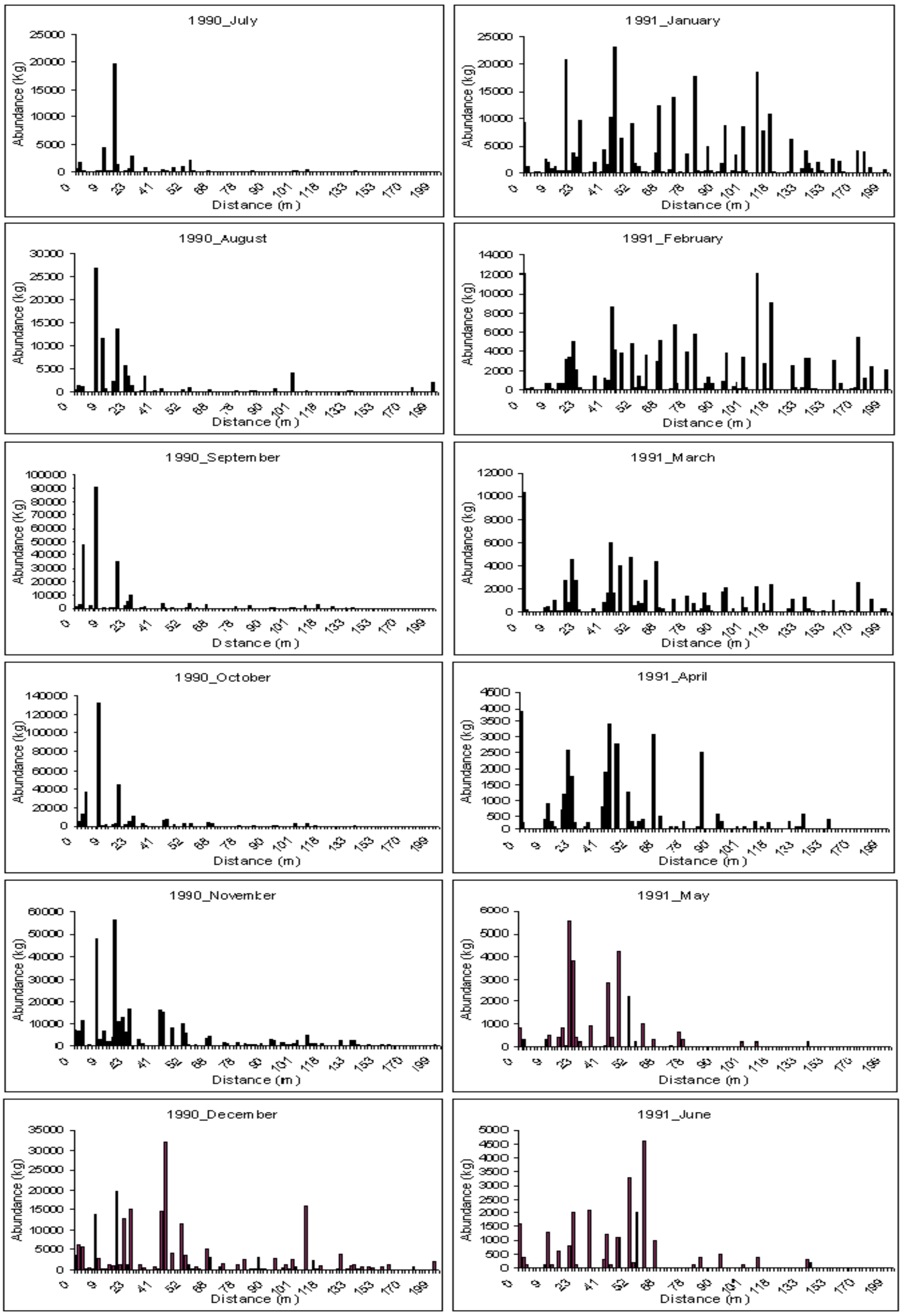


Fig. 6 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1990, starting in July and finishing in June of the following year, 1991.

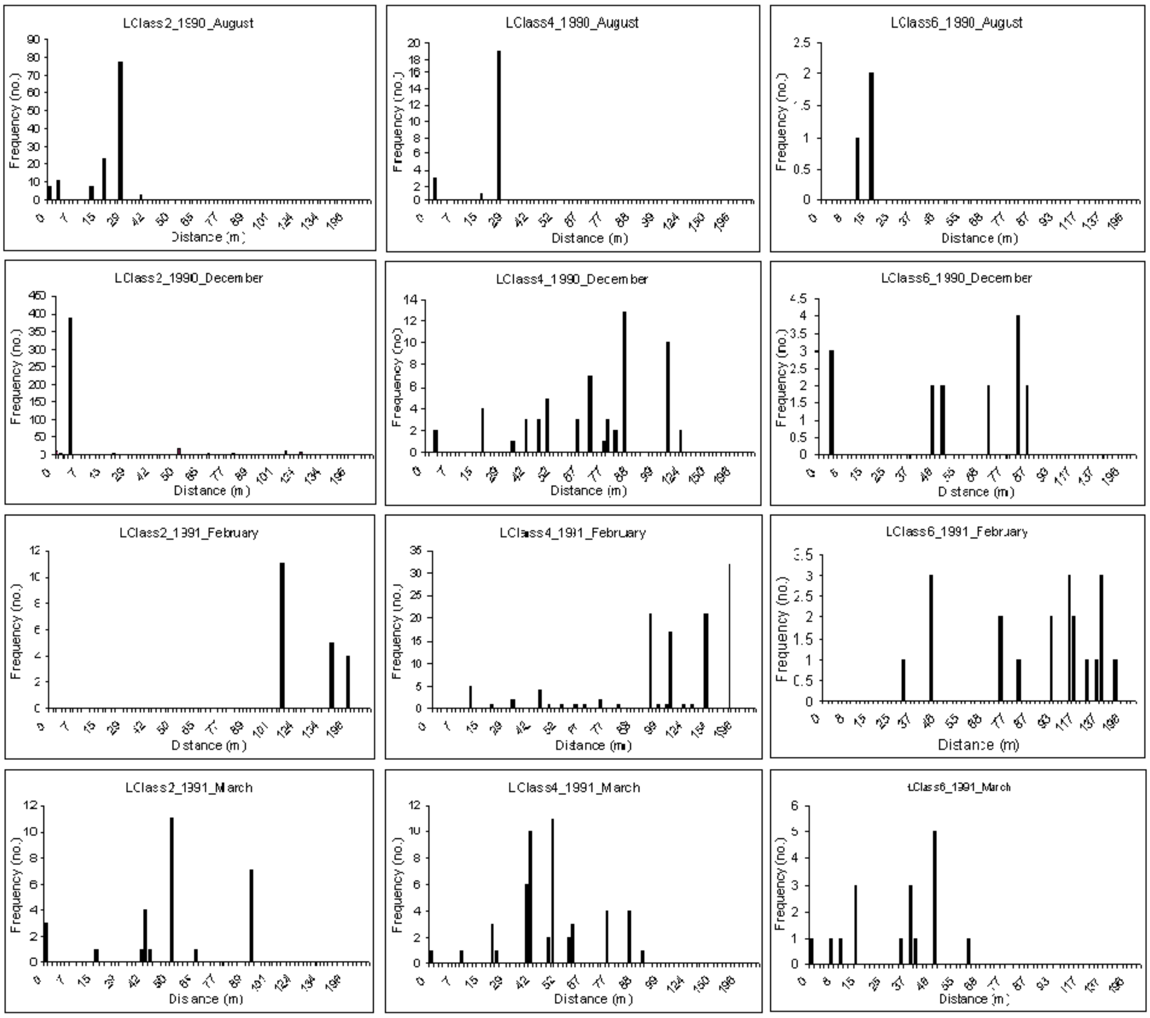


Fig 7. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left, from 1 to 4.5 cm), 4 (middle, from 15 to 19 cm) and 6 (right, from 25 to 29 cm), occurrence frequency for each month of 1990, starting in July and finishing in June of the following year, 1991.

The analysis of the residual graphics of the models A and B for autumn/early winter reveal some pattern, in that the majority of residuals are situated where the fitted values are lower, but this reflects the distribution of the data rather than a poorly fitted model. Therefore, given the significance values of the smoothers and the "good" residual distribution, it seems that the GAMM approach is appropriate and fits the data.

Table I - Approximate significance values of smooth terms, Akaike Information Criterion (AIC), square R and number of observations used in the GAMM obtained from each length class of each haul as response variable. The GAMM was fitted for 4 seasons, summer (June to October), autumn/early winter (November and December), winter (January and February) and spring (March and April).

		Model A			
		Summer	Autumn/Winter	Winter	Spring
***p*-value**	Distance	3.27e-06	2e-16	2e-16	7.66e-15
	Depth	2e-16	5.84e-08	4.99e-06	2e-16
	SST	2e-16	1.88e-10	6.27e-05	7.65e-09
Df	Distance	2.588	8.062	1.000	1.000
	Depth	6.903	5.145	5.689	7.006
	SST	7.500	1.608	2.862	6.904
F	Distance	6.031	12.553	128.754	61.135
	Depth	19.855	5.754	4.611	10.760
	SST	12.952	12.943	4.864	6.287
AIC		6721.291	22671.19	10144.30	18465.83
R-sq		0.33	0.0291	0.128	0.108
No. observations		1024	3102	1435	2636

Table II - Approximate significance values of smooth terms, Akaike Information Criterion (AIC), square R and number of observations used in the GAMM obtained from the average length class of each haul as response variable. The GAMM was fitted for 4 seasons, summer (June to October), autumn/early winter (November and December), winter (January and February) and spring (March and April).

		Model B			
		Summer	Autumn/Winter	Winter	Spring
***p*-values**	Distance	0.069	0.00120	7.26e-12	1.20e-07
	Depth	6.61e-06	0.00203	0.0405	4.80e-06
	SST	5.45e-07	0.13455	0.1824	2.93e-05
Df	Distance	1.000	3.927	1.000	1.000
	Depth	4.313	1.000	3.236	4.928
	SST	6.433	1.000	1.000	4.562
F	Distance	3.344	3.283	50.352	28.819
	Depth	4.885	9.639	2.124	4.718
	SST	5.687	2,248	1.785	4.200
AIC		1329.231	2873.046	2305.494	3586.650
R-sq		0.325	0.0823	0.15	0.186
n		207	425	354	535

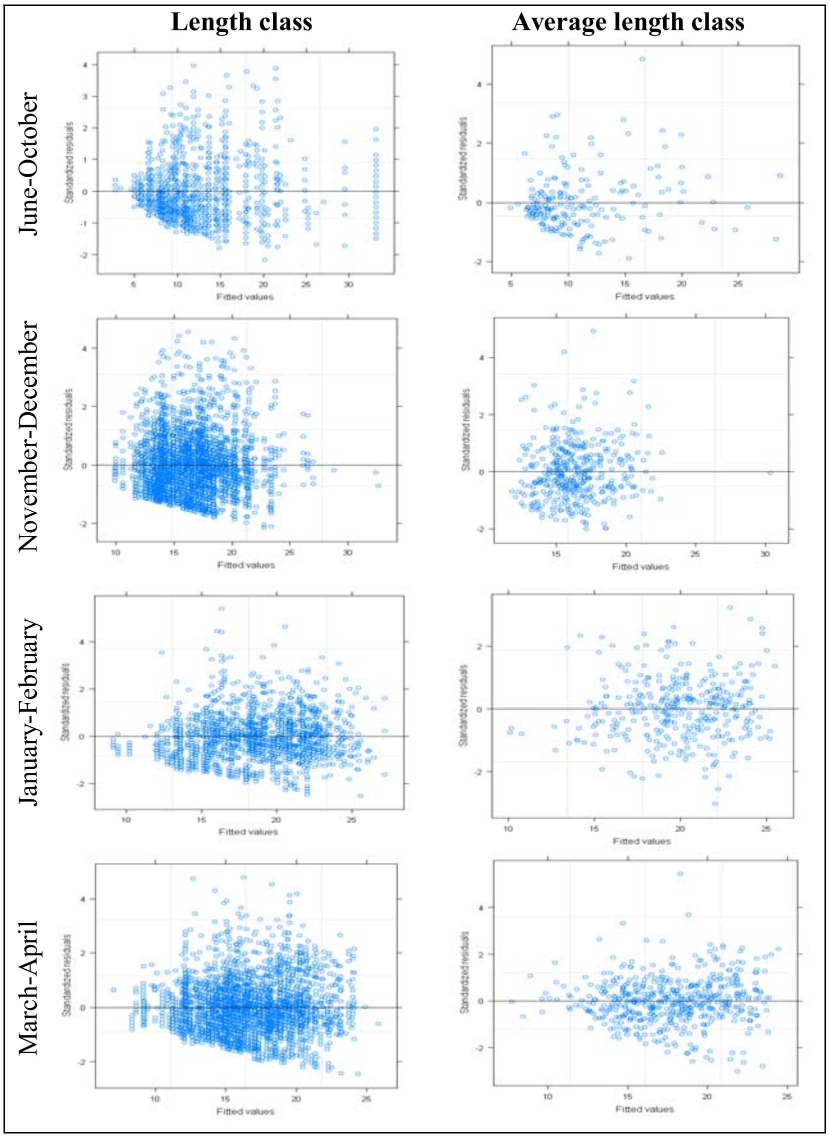


Fig. 8 – GAMM residuals dispersion. Standardized residuals (y-axis) for both datasets, length class and average length class of each haul as a response variable, against the fitted values (x-axis) of the models.

The residual graphics of the two models are shown, in order to compare their goodness of fit. Because these are very similar and because GAMM smooth curves in both models of survey data are also very alike, only the results of model A (Fig.9) are shown in this section as an example (see Appendix VII for model B). GAMM results for all the explanatory variables show smoothing curves with 95% confidence limits. The main trends evident from the smooth curves of the most significant effect in most seasons, distance to coast, reveal a more important effect up to 80 miles from the coast. In winter and spring an inverse relationship seems to exist between length and distance to coast, in that bigger squid tend to be closer to the coast. However, in summer this relationship seems to be the opposite, although distance is not the most significant explanatory variable in this season. In the transition between these seasons, in autumn/early winter, distance to coast is in fact the most significant variable but its smoothing curve does not show any clear trend. In general, it seems that the relationship is the same as in summer, however the complex shape of the curve does not allow a clear interpretation.

The effect of depth, in all the seasons, seems to be more important in shallow waters since it is positive in the range between 75 and 250m, with a limit around 150m in autumn and winter. Therefore, below the 250m, depth seem to have no influence in squid size distribution although the wide confidence limits for deeper water may, to some extent, reflect lower data availability rather than the absence of any relationship with depth. Within the limits of positive effect of depth (i.e. in waters <250m deep), size seems to have a relative direct relation with depth, larger sizes in deeper waters. However, this pattern is not consistently seen for depths between 50 and 100m: in spring the opposite trend is apparent and in summer this relationship is linear.

The smoothing curves for sea surface temperature show a more important effect in temperatures above 8ºC. In summer, when temperature is one of the most significant parameters, until 11ºC, smaller squids appear with lower temperatures. However, above ~11ºC this relation inverts, which reveals a peak of size around 11ºC. In autumn small squid also appear in lower temperatures, however in winter, as temperatures are very low, the positive effect is registered only between 8 and 9ºC and they seem to prefer the warmer waters. In spring, above 8ºC the relationship between temperature and squid length is apparently linear but again temperatures are very constant and low.

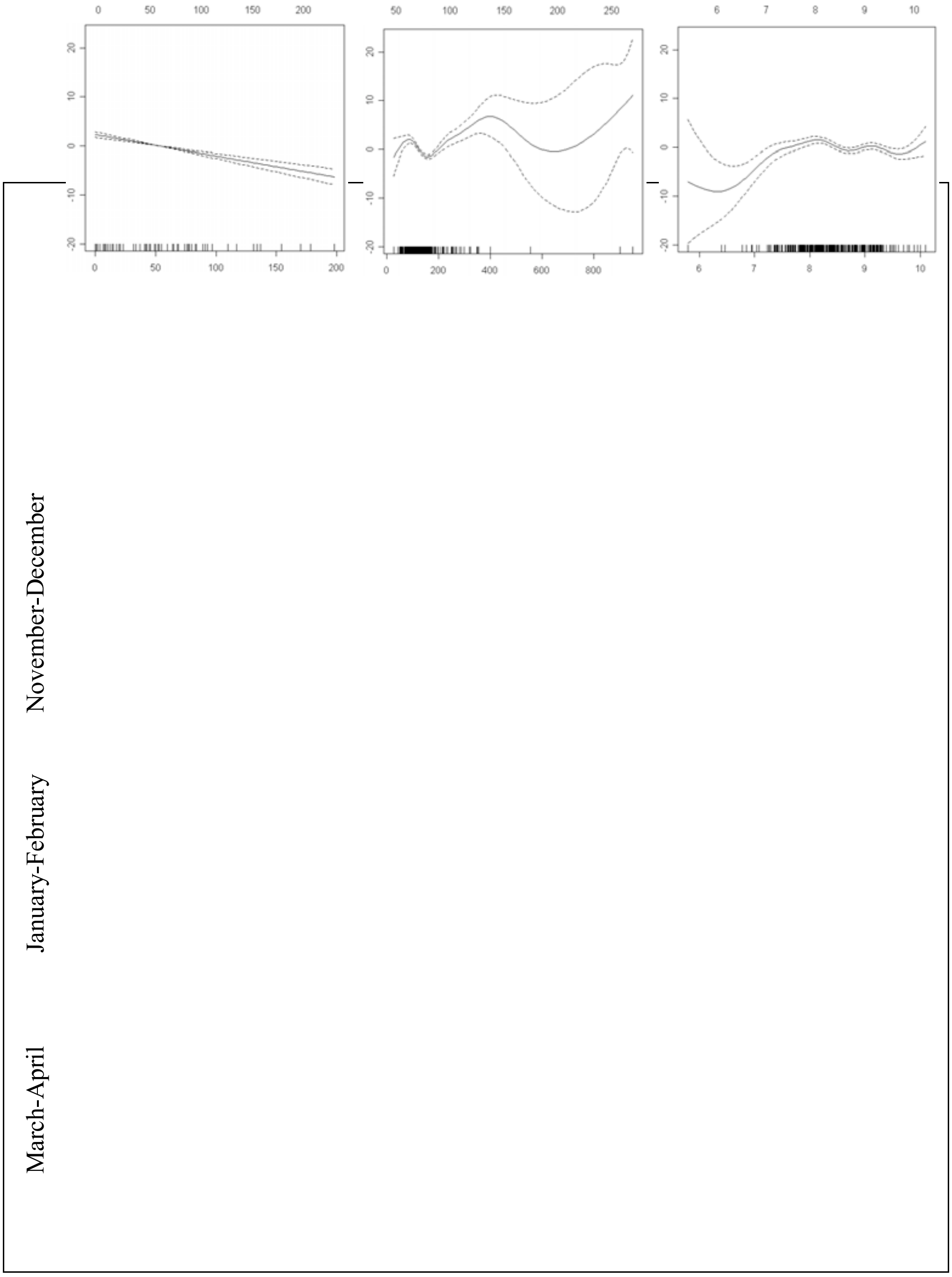


Fig. 9 – GAMM results on dataset with each length class of each haul as a response variable. Squid length class is represented as a function of the smooth terms, distance to coast depth and SST for each season. Dashed lines represent two standard error boundaries around the main affects.

3.3.b. When modelling fishery data with a presence/absence approach, effects of all explanatory variables are equally and highly significant in all months (Table III), with the exception of depth in September and June for which higher *p*-values were seen, although still very significant ($p<0.001$). The model also shows very similar degrees of freedom throughout the examined months for all variables, ~1-8, although SST have the lower values, ~1-5, indicating almost linear relationships. This analysis reveals therefore that all studied environmental conditions are important to determine squid presence.

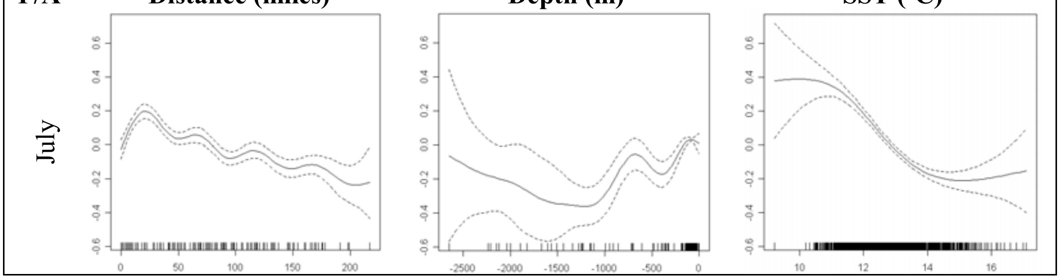
The smoothing curves obtained with presence/absence of landings as the response variable (Fig. 11), reveal a clear and consistent trend throughout the months for distance to coast, SST and bathymetry. There is one exception to this, for depth in July, August and September that seems to reveal no positive effects due to wide confidence limits. The smooth term for distance to coast indicates an important effect of distance on veined squid presence throughout the fishing area but the trend disappears for hauls farther from the coast, beyond approximately 175 miles. These smooth curves reveal that, in all months, *L. forbesi* is present until 25 miles from the coast and begins to disappear after this once a peak is seen at this distance. Bathymetry only has a positive, but strong, effect between 0 and 200m depths, where abundance increases with depth. SST smooth curves reveal an optimal temperature peak of abundance around 10°C and from this temperature abundance decreases with the increase of temperature.

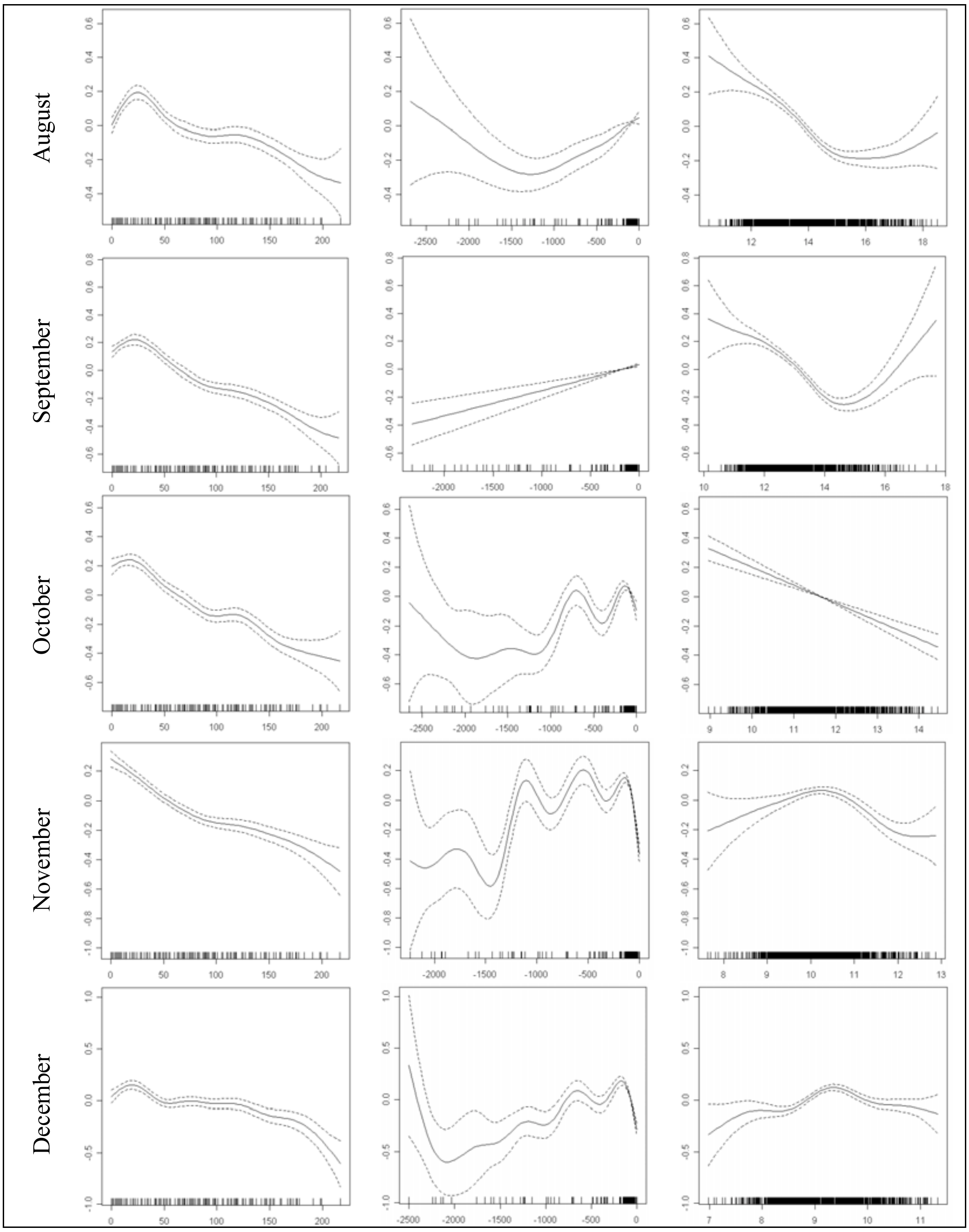
When modelling abundance (given presence) data, the results show some similar trends to presence/absence model, but not in all months. With the exception of variable depth in August, October and June and SST in July, all explanatory variables in all months are highly significant, especially distance to coast (Table IV). Apart from depth in June, these reported exceptions are still significant although with higher *p*-values, near 0.001. The degrees of freedoms of the models, are low between ~1 and 8, and the explanatory variable “distance to coast” demonstrates values of approximately 1 in all months. The significance values of the smooth terms reveal therefore a good fit of the model that is also seen in standardized residual graphics (Fig. 11) since these show no important trends. This analysis reveals that all environmental variables, especially distance to coast, influence *L. forbesi* abundance in the IVa and b and VIa ICES subdivisions.

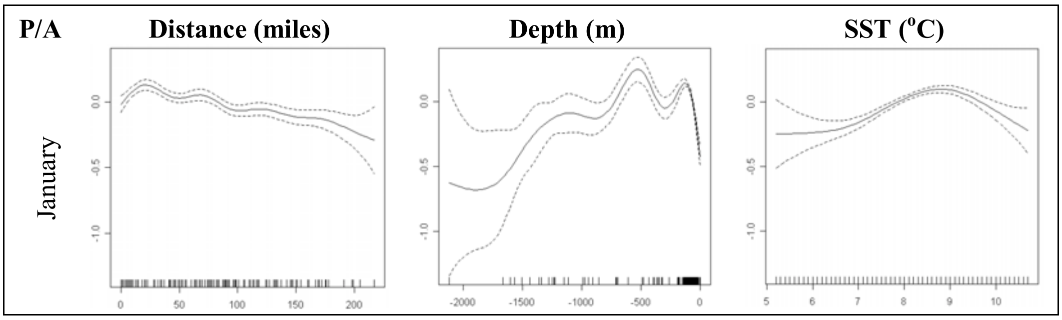
GAMM smooth curves of presence data derived from Scottish fisheries (Fig. 12) show very specific patterns and positive effect of the variables throughout the months, in part similar to those found in presence/absence model but quite different, in some months, to those found in when modelling survey data to relate size distribution with environmental conditions. This presence model shows that abundance increases towards the coast in all months and the effect of the smoother begins to be negative from 175 miles from the coast, just as in the presence/absence model, and confidence limits become wider. Depth reveals the most important positive effect on abundance between 0 and 200m and between these values veined squid abundance increases greatly with depth. However, between June and August to October, confidence limits are too wide to reveal any positive. Finally, the SST smoothing curve demonstrates a positive influence of temperatures around 8 and 12°C, allowing for one or two °C of difference according to the season, but as a general pattern, abundance increases from 7-8°C until ~10°C when it starts to decrease, again as previously seen in the presence/absence model.

Table III - Significance values of smooth terms, Akaike Information Criterion (AIC), square R and number of observations used in the GAMM obtained from presence/absence landings data. GAMM was fitted for all months, from July to June, with all years combined.

P/A	Distance	Depth	SST	AIC	R-sq	n
Jul	*p*=2e-16 Df=8.102 F=16.87	*p*=2.4e-15 Df=6.791 F=10.06	*p*=2e-16 Df=4.628 F=28.74	2630.144	0.099	2655
Aug	*p*=2e-16 Df=6.965 F=17.67	*p*=2.2e-11 Df=3.196 F=9.267	*p*=2e-16 Df=4.454 F=19.20	2879.897	0.0077	2607
Sep	*p*=2e-16 Df=6.003 F=41.29	*p*=1.61e-07 Df=1.000 F=27.61	*p*=2e-16 Df=5.161 F=25.06	2983.174	0.0716	2512
Oct	*p*=2e-16 Df=6.440 F=37.50	*p*=2e-16 Df=7.552 F=12.17	*p*=7.03e-15 Df=1.000 F=61.36	2796.13	0.064	2450
Nov	*p*=2e-16 Df=4.151 F=21.665	*p*=2e-16 Df=8.502 F=24.430	*p*=7.49e-15 Df=4.749 F=9.789	2575.079	0.116	2502
Dec	*p*=2e-16 Df=7.280 F=11.34	*p*=2e-16 Df=8.101 F=21.56	*p*=2e-16 Df=6.351 F=11.13	2053.722	0.123	2249
Jan	*p*=2.24e-15 Df=7.243 F=10.10	*p*=2e-16 Df=8.491 F=23.70	*p*=2e-16 Df=4.646 F=10.85	2056.974	0.201	2366
Feb	*p*=2e-16 Df=7.640 F=13.33	*p*=2e-16 Df=8.429 F=23.27	*p*=2e-16 Df=5.958 F=22.24	2480.834	0.223	2702
Mar	*p*=3.99e-13 Df=4.008 F=8.788	*p*=2e-16 Df=8.629 F=36.605	*p*=2e-16 Df=5.853 F=21.541	2578.621	0.243	2633
Apr	*p*=2e-16 Df=6.137 F=12.41	*p*=2e-16 Df=8.223 F=27.69	*p*=2e-16 Df=5.572 F=20.26	2666.174	0.233	2596
May	*p*=2e-16 Df=6.139 F=18.50	*p*=2e-16 Df=7.993 F=21.55	*p*=2e-16 Df=5.452 F=16.85	2843.938	0.197	2623
Jun	*p*=2e-16 Df=7.227 F=22.527	*p*=1.91e-08 Df=6.995 F=6.053	*p*=2e-16 Df=3.492 F=14.504	2832.598	0.0458	2565




August
September
October
November
December


P/A
Distance (miles)
Depth (m)
SST (°C)
January

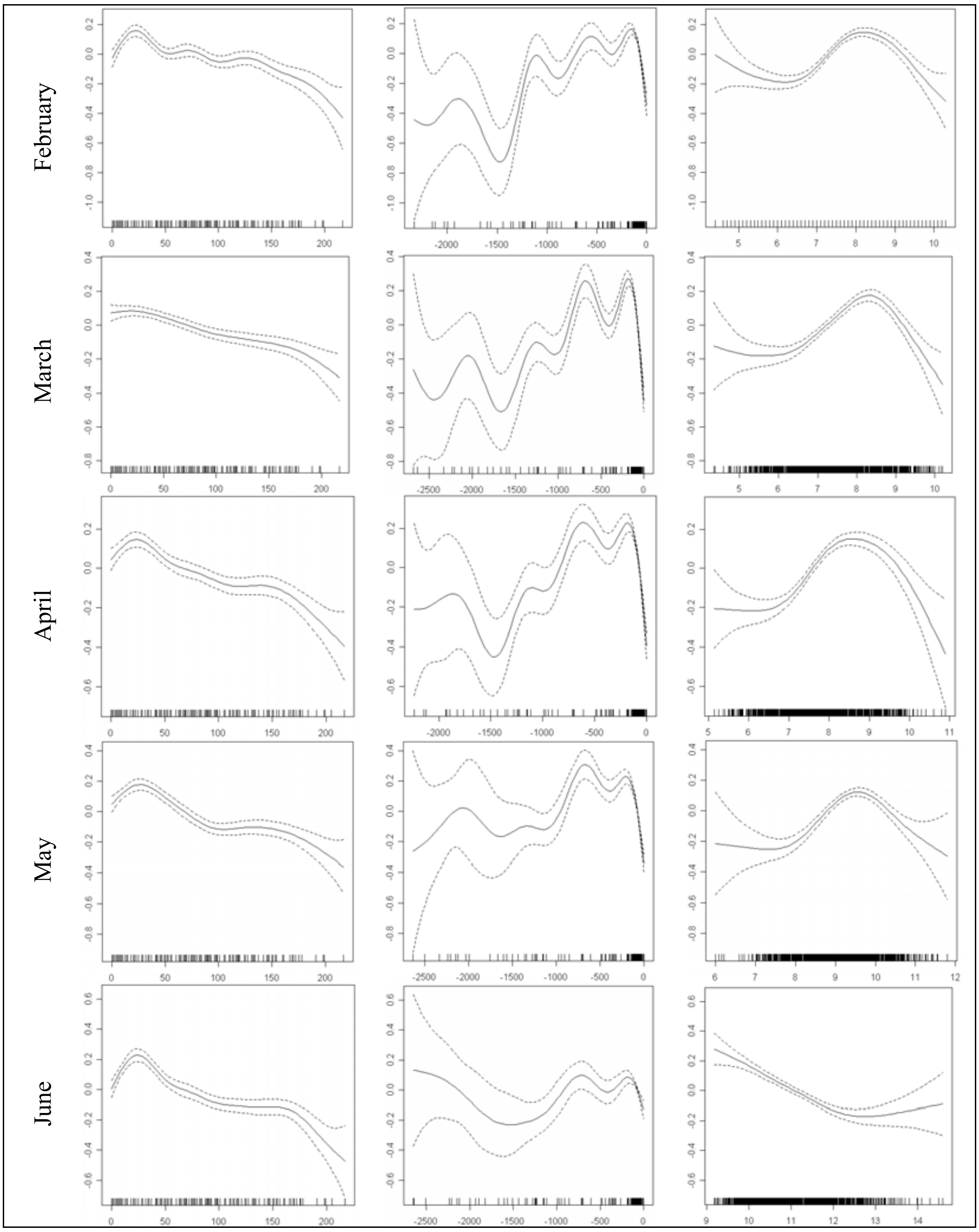
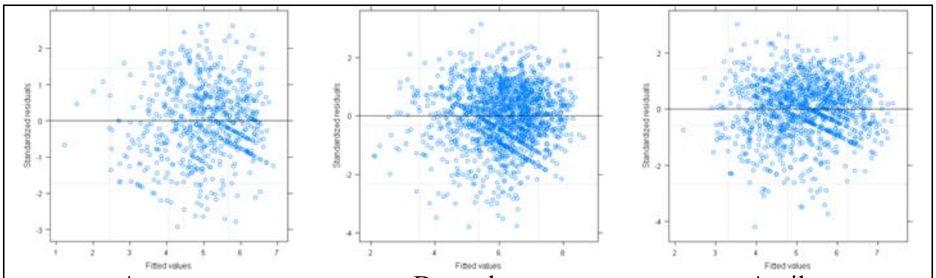


Fig. 10– Landings presence/absence GAMM results. Veined squid landings are represented as a function of the smooth terms, distance to coast depth and SST for each month. Dashed lines represent two standard error boundaries around the main affects.

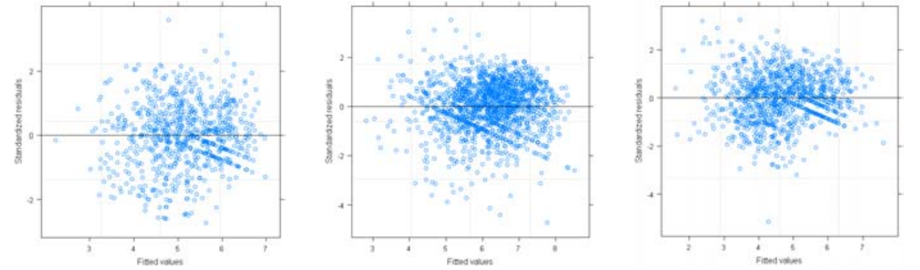
Table IV - Significance values of smooth terms, Akaike Information Criterion (AIC), square R and number of observations used in the GAMM obtained from presence landings data. GAMM was fitted for all months, from July to June, with all years combined.

Presence	Distance	Depth	SST	AIC	R-sq	n
Jul	*p*=2e-16 Df=1.000 F=73.462	*p*=2.1e-05 Df=5.113 F=4.264	*p*=0.00017 Df=1.000 F=14.290	2936.355	0.134	712
Aug	*p*=8.72e-06 Df=1.000 F=20.04	*p*=0.000202 Df=3.198 F=4.09	*p*=1.86e-05 Df=5.649 F=4.29	3222.792	0.089	781
Sep	*p*=2e-16 Df=1 F=96.14	*p*=6.68e-06 Df=1 F=20.49	*p*=2e-16 Df=1 F=73.41	4238.337	0.15	1049
Oct	*p*=2e-16 Df=1 F=360.55	*p*=0.000269 Df=1 F=13.34	*p*=2e-16 Df=1 F=163.40	5724.713	0.242	1448
Nov	*p*=2e-16 Df=3.971 F=22.531	*p*=2e-16 Df=7.730 F=14.432	*p*=8.4e-15 Df=6.262 F=9.839	6333.957	0.214	1674
Dec	*p*=5.21e-15 Df=1.148 F=23.71	*p*=2e-16 Df=8.483 F=25.10	*p*=2e-16 Df=5.062 F=13.18	5920.849	0.19	1593
Jan	*p*=7.1e-16 Df=2.333 F=16.48	*p*=2e-16 Df=8.524 F=45.78	*p*=2e-16 Df=4.774 F=14.53	5728.058	0.244	1540
Feb	*p*=1.25e-12 Df=1.000 F=51.34	*p*=2e-16 Df=8.466 F=26.34	*p*=3.07e-15 Df=3.710 F=11.06	5179.785	0.2	1418
Mar	*p*=9.29e-12 Df=1.000 F=47.35	*p*=2e-16 Df=7.983 F=13.40	*p*=1.68e-11 Df=2.952 F=10.59	4731.185	0.152	1284
Apr	*p*=3.05e-16 Df=1.000 F=68.926	*p*=2e-16 Df=7.358 F=12.077	*p*=5.28e-06 Df=3.463 F=5.325	4180.406	0.168	1085
May	*p*=5.53e-13 Df=1.000 F=53.590	*p*=9.15e-06 Df=5.955 F=4.476	*p*=2.83e-08 Df=4.397 F=6.052	3746.745	0.121	901
Jun	*p*=1.17e-10 Df=2.995 F=10.010	*p*=0.00857 Df=2.098 F=3.117	*p*=5.98e-08 Df=3.391 F=6.879	3208.371	0.094	771

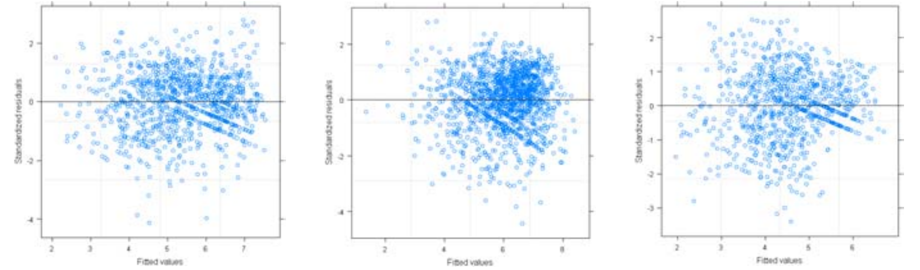
July	November	March



August December April



September January May



October February June

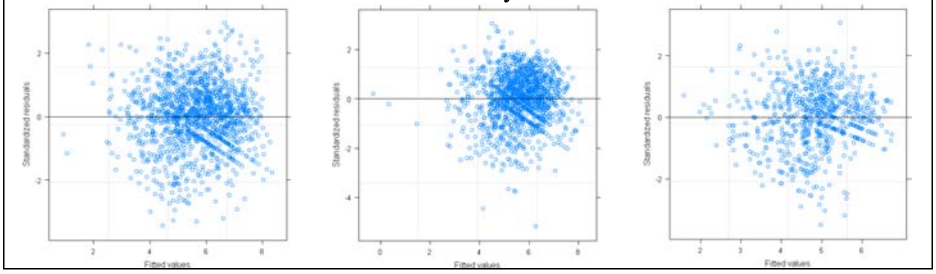
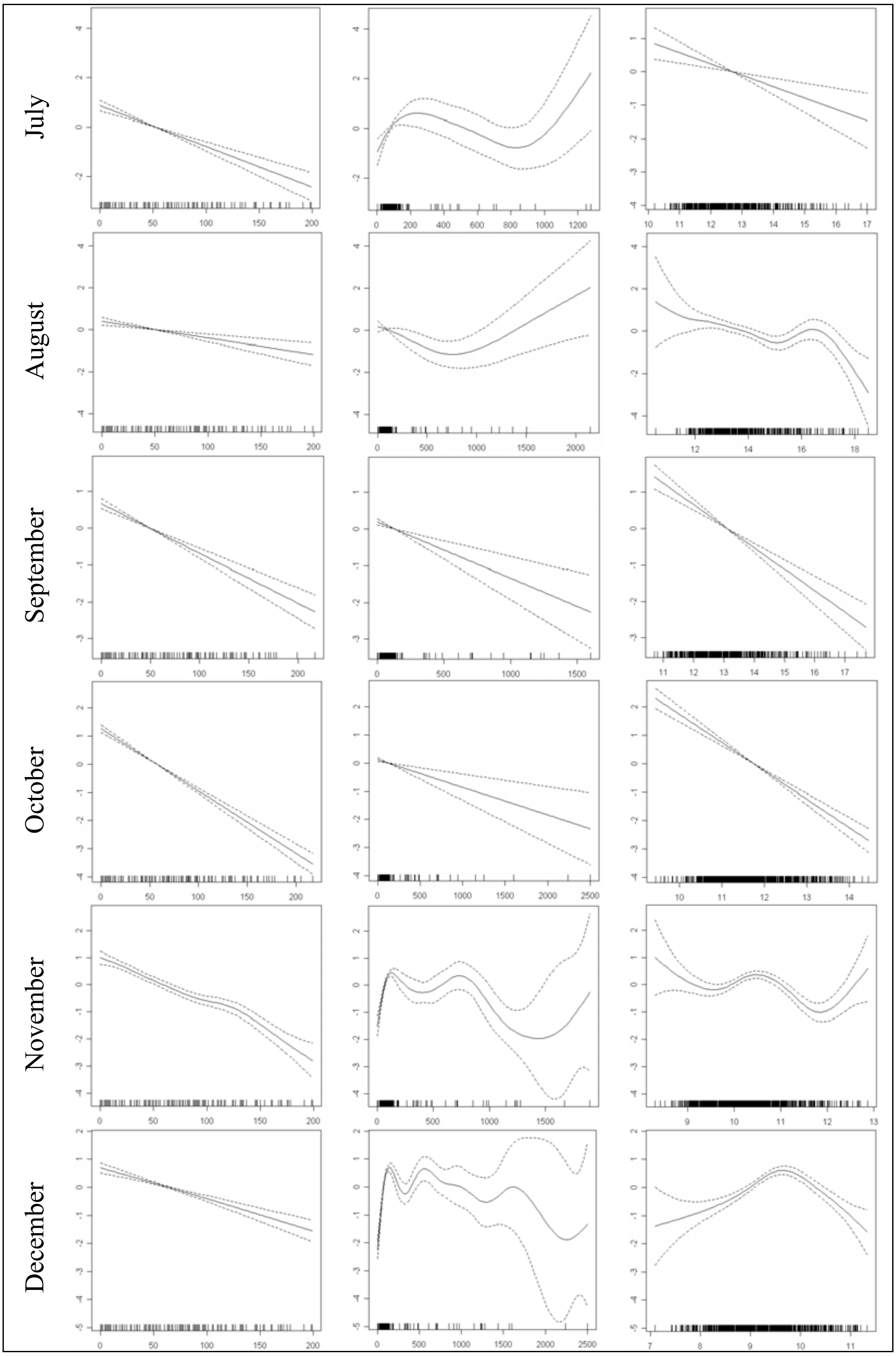


Fig 11 – GAMM residuals dispersion of presence landings data. Standardized residuals (y-axis) plotted against the fitted values (x-axis) of the model for all months.

Distance (miles)	Depth (m)	SST (^{o}C)


July
August
September
October
November
December
0 50 100 150 200
0 200 400 600 800 1000 1200
10 11 12 13 14 15 16 17
0 50 100 150 200
0 500 1000 1500 2000
12 14 16 18
0 50 100 150 200
0 500 1000 1500
11 12 13 14 15 16 17
0 50 100 150 200
0 500 1000 1500 2000 2500
10 11 12 13 14
0 50 100 150 200
0 500 1000 1500
9 10 11 12 13
0 50 100 150 200
0 500 1000 1500 2000 2500
7 8 9 10 11

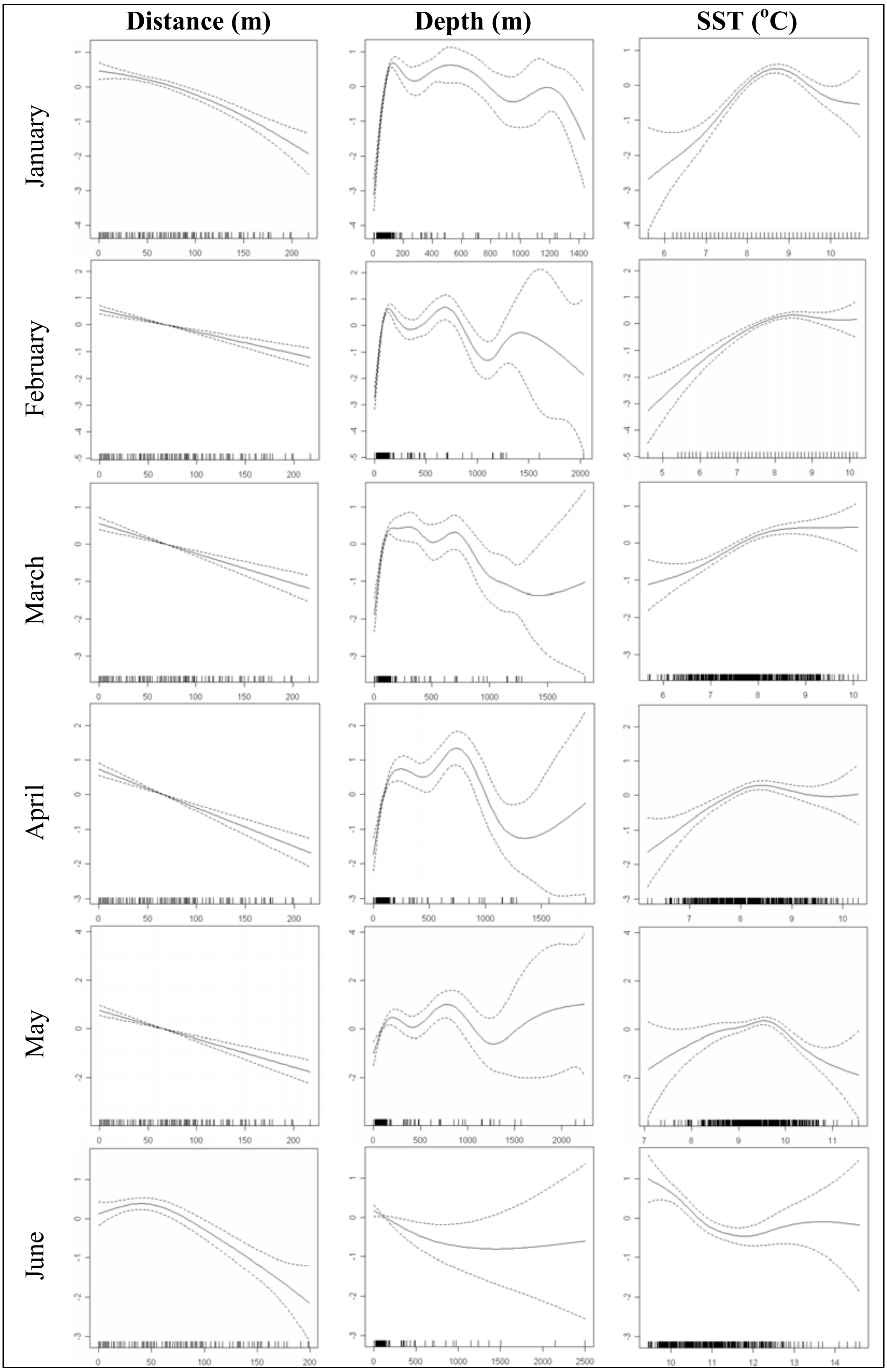


Fig. 12– GAMM results with using presence landings data. Veined squid landings were log (ln) transformed and are represented as a function of the smooth terms, distance to coast, depth and SST for each month. Dashed lines represent two standard error boundaries around the main affects.

4. Discussion

4.1. West Coast to North Sea migrations

4.1.a. The spatial distribution of Scottish squid catches broadly reflects the distribution of fishing activity, although very little of this activity is directly targeted at cephalopods (Pierce *et al.,* 2001). Seasonal shifts in the distribution of squid catches are therefore largely due to changes in its distribution and abundance; thus shifts in catch distribution can help to track the recruitment, migration and spawning patterns of the species (Caddy, 1983).

Monthly GIS maps of abundance of *Loligo forbesi* were the first approach used to verify the first hypothesis, similar to the approach used in a study of the migratory squid *Illex argentinus* from the southwest Atlantic waters performed by Sacau *et al.* (2005). Even if abundance and distribution of a cephalopod stock may fluctuate widely from year to year, because each year's stocks consist mainly of new recruits (Bellido *et al.,* 2001), the analysis of the GIS maps revealed that this species does not routinely migrate from west coast to east coast of Scotland during winter and back to west coast in spring, as previously suggested by Waluda and Pierce (1998). If such movement exists a clear peak of abundance is expected in the West Coast of Scotland during November and December, and around January and February the abundance peak should appear more close to North Sea, the possible spawning area (Waluda and Pierce 1998, Pierce *et al.,* 2001; Young *et al.,* 2006*a*). During spring, the abundance peak should disappear from North Sea and appear almost exclusively on the West Coast and then move to the North Sea again in autumn to recruit. However, the lack of this pattern in the data analysed during the present study is evidence against such movement.

Two main technical differences were found between Waluda and Pierce (1998) and the present work that could lead to the difference in the results. The fundamental discrepancies are that Waluda and Pierce (1998) used landings per unit effort (LPUE) as an abundance index and mapped data for each ICES rectangle as an isolated abundance point. On the other hand, in the present work, landings are used as abundance index and contour maps were built instead. Both methods have advantages and disadvantages, however the choice of different abundance indexes seems not to change the patterns in the 5 years of common analysis, as predicted after the comparison between these two approaches revealed great similarities, earlier in this work (see methods 3.1.a). It is possible that when using the contour technique to create abundance maps, some values can be omitted because neighbouring abundance values are combined to create the contours. However, abundance and location of cephalopod populations is highly influenced by the prevalence and scale of their migrations and therefore these migrations involve transfer of hundreds of millions of individuals during phases of high growth (Boyle and Boletzky, 1996), just as dense aggregations are encountered in *L. gahi*, mainly during the offshore feeding period (Hatfield and des Clers, 1998). These possible omissions are not therefore considered important. When creating maps using each rectangle as isolated point, there is no omission of values however the visual interpretation is significantly more difficult, since the visual gradient is in the size of the abundance symbol and therefore high and low abundance are spatially mixed.

Apart from these difficulties and small differences due to divergent techniques, as briefly mentioned above, the analysis of the small five year series used in Waluda and Pierce (1998) reveals no contradictory results with the present work, since for those few years the patterns are quite similar in both studies. However, when expanding the analysis for twenty years, it is clear that the pattern is not consistent throughout and consequently it is not possible to conclude that Scottish *L. forbesi* migrate from the West Coast to the North Sea in the winter, and back to west coast in spring, or indeed show any other type of consistent migration pattern. A relative constant pattern in optimal environmental conditions, a fishery tendency once the major directed squid fishery occurs between October and January in Northeast of Scotland (Bellido *et al.,* 2001, Chen *et al.,* 2006), or a possible inflow of squid into Scottish waters from further south, as Pierce and Boyle (2003) suggested for example due to the strong coastal current flow along the West Coast of Scotland that increases nutrient supplies in the area, might be some reasons that led to the apparent migration pattern, described by Waluda and Pierce (1998), in those studied five years. In these years, the major *L. forbesi* abundance peak in Scottish waters was registered (Zuur and Pierce, 2004), possibly due to the mildest winter climate seen in the North Sea for 50 years (Becker and Pauly, 1996), which could influence squid distribution because, as poikilothermic species, they are affected by water temperature (Pierce *et al.,* 1998; Sims *et al.,* 2001; Bellido *et al.,* 2001).

The GIS maps of veined squid abundance also reveal a spatially restricted peak of abundance to the North of Scotland, around June, followed by a spatial expansion of abundance when approaching the winter season. Although the pattern is not evident in every year, it seems that squid abundance in the North Sea, between April and July, is very low; however on the West Coast, the abundance is also very low. *L. forbesi* seems therefore to concentrate to North of Scotland, which constitutes a possible spawning and/or recruitment site. One final observation of these maps was two distinct abundance peaks, either in different coasts or in the same but one much further south than the other. This can suggest that the two described veined squid cohorts (Collins *et al.,* 1997, 1999; Zuur and Pierce, 2004, Pierce *et al.,* 2005) might have different migratory behaviours as Arkhipkin *et al.* (2004) discussed for the migratory squid *L. gahi*. However, these two abundance peaks are not visible in all years and therefore it is not possible to detect any clear pattern. One other possibility is the migration of the English *L. forbesi* cohort into more northern waters in some years, since Sims *et al.* (2001) reported that according to environmental condition this species could vary its migration range.

4.1.b. Although the GIS maps seem to be quite consistent in revealing an absence of migratory movements of *L. forbesi* from the West Coast of Scotland to the North Sea, or any other consistent movement pattern, some uncertainties regarding the technique applied and the complexity of data might still remain. Therefore in support of the suggestion of non-migratory behaviour, the length frequency analysis performed using survey data revealed a similar result, i.e. that there is no consistent migration pattern from one coast to another as Waluda and Pierce (1998) suggested.

From this analysis, as was expected since summer-autumn is the most important recruitment season, the time series graphics revealed the presence of small to medium-sized animals in August in the North Sea (NS). When approaching November/December on the West coast (WC), squid length is expected to increase, and to continue to increase in January/February (NS), because winter is suggested to be the most important spawning season (Collins *et al.* (1997). Since size and maturity are positively related (Wood, 2000; Pierce *et al.,* 2001), these breeders should belong to the higher length classes. On the other hand, later on in spring (April), the first wave of recruitment (i.e. smaller animals) is expected to appear on the west coast (Pierce *et al.,* 1994). However this size gradient pattern was not apparent. In August (in the North Sea) most animals present were small (length class 2), but when approaching winter it seems that the growth is not consistent throughout the examined years, and it also seems that in spring the existence of small squids is not regular.

Nevertheless, *L. forbesi* life cycle is more complex than described above. According to Collins *et al.* (1997, 1999), Zuur and Pierce (2004) and Pierce *et al.* (2005), veined squid have two spawning seasons, in winter (around January) and in summer, although the latter is not important as the first. Two recruitment seasons also occur in Scottish waters, the most important in late summer/autumn and the other in spring. Therefore the presence of almost exclusively length class 2 (5-9.5cm) in August is evidence of the already described summer recruitment season, future winter spawners (Pierce *et al.,* 2005), because according to Pierce *et al.* (1994*b*) full recruitment to the fishery occurs at a mantle length of approximately 15cm. This length frequency analysis can also reinforce the suggestion of a second recruitment season since length class 1 or 2 animals were also present in other seasons. However, there was no other peak of recruitment that was as clearly defined as in autumn, which can also indicate that recruitment season is extended for several months as suggested by Lum-Kong *et al.* (1992) and Boyle *et al.* (1995). The existence of two (or more) cohorts (or micro-cohorts) in the same sampling area can however interfere with the length frequency analysis, hiding possible size distribution patterns within cohorts. Other factors can affect with the ease which results of this analysis can be interpreted, such as the possible reduction of female size during spawning season (Collins *et al.,* 1997), the highly variable growth rates - veined squid reveal for example (at least) two sizes at maturity (Pierce *et al.*, 1994, Collins *et al.,* 1999; Smith *et al.,* 2005), and also the incorrect identification of small squid. It has been reported that sometimes the loliginid *Allotheutis* can be confused with small *L. forbesi* in fisheries data, since species ID is not confirmed, however in survey samples this identification is confirmed although some errors are suspected to be made (Pierce *et al.,* 2005).

4.2. Inshore/Offshore migrations

4.2.a. Mangold-Wirz (1963) stated that demersal and near-bottom adult squid make their feeding and spawning migrations over the bottom in offshore–onshore directions and studies of other squid species, such as *L. pealeii* from the northern United States (Hatfield and Cadrin, 2001) or *L. gahi* from the SW Atlantic, suggest a movement from their nurseries in shallow inshore waters to feeding offshore grounds in deeper waters (Hatfield and Rodhouse, 1994). The hypothesis of an inshore-offshore migration in Scottish *L. forbesi* was considered in the present study, analysing monthly distance of centres of abundance to the coast. Between autumn (around August/September) and early winter (around December), higher abundance of squid was expected in offshore waters, as Holme (1974) and Sims *et al.* (2001) reported for English *L. forbesi* that migrates to inshore grounds during summer and to offshore grounds when autumn approaches. However, the Scottish veined squid seems to have a different behaviour from the English because in general, between May and October (spring and summer), they tend to be closer to coast, in inshore grounds, and between November and April (autumn and winter) they appear in offshore waters, although never completely disappearing from the inshore grounds. In some years, high squid abundance appears in offshore grounds one month earlier or later, but this pattern is revealed to be rather consistent between years.

In Scottish and Irish waters, two breeding populations are reported, that correspond to two distinct recruitment peaks (Collins *et al.,* 1997, 1999; Zuur and Pierce, 2004, Pierce *et al.,* 2005). The main recruitment period, in late summer and the beginning of autumn, can be derived from the winter spawning, and the spring recruitment period from the summer breeder population (Collins *et al.,* 1997; Pierce *et al.,* 2005); therefore the pattern emerging from the present abundance graphics suggests that the summer spawning season takes in inshore waters, as well as autumn recruitment. However, where winter breeders' spawn and spring recruitment occurs is not clear. Boyle *et al.* (1995) proposed a less defined life cycle, where individual squid may live 18 months or longer and the spawning season can be extended to several months; in this case squids from winter breeders become the summer spawners of the following year. According to this life cycle, recruitment seasons can also be extended and are not seasonally well defined, although it seems that spring recruitment season is apparently more important than the autumn season. The present study suggests that summer spawning occurs in inshore areas but otherwise the location of recruitment and other spawning sites are unclear.

Arkhipkin and Middleton (2002) discussed a possible interaction between two different species, *L gahi* and *I. argentinus*, with distinct migratory behaviours around the Falkland waters, and Agnew *et al.* (1998) reported that, in *L. gahi*, a changeover between the two cohorts has been indicated by a decline in the overall maturity status of squid, usually in April–May. Therefore, when one cohort is in offshore areas to feed the other is in inshore waters to spawn and this arrangement changes when the maturity season of the offshore cohort arrives (Arkhipkin *et al.,* 2004). Although genetic studies found that *L. forbesi* on the continental self of the Northern Europe appears to be one single population (Shaw *et al.,* 1999), two distinct cohorts were identified and evidence of genetic resemblance between immature squid from the two recruitment periods is missing (Zuur and Pierce, 2004). These spatial patterns in landings can therefore reveal different migratory behaviors, while one cohort migrates to offshore grounds around November; the other is resident in inshore areas. This would explain the occurrence of a significant level of abundance near the coast all year around and a very low or zero abundance in offshore grounds, during some seasons. The complete life cycle of the resident cohort would occur in inshore grounds, however the migratory cohort, if winter breeders, would spawn offshore and recruit in inshore waters during autumn, and if summer breeders, would spawn inshore and recruit offshore during spring. This possible migratory cohort can be either from coastal waters, interacting with the non-migratory cohort between May and October, or can migrate to these reported offshore areas from the south as Pierce and Boyle (2003) discussed, or elsewhere (Zuur and Pierce, 2004).

4.2.b. According to Zuur and Pierce (2004) the mis-match in abundance trends, for autumn recruits and winter breeders in Scottish waters, could indicate that part of the adult spawning population migrates into Scottish waters from elsewhere in winter rather than arriving as immature animals in the autumn. As an estimate of recruitment can be derived from a size frequency distribution, length frequency analyses are often used to assess these inshore-offshore and east-west migrations of fished populations, including *Loligo* species (Powell, 2006). Although methodological differences between surveys vessels cannot be certainly excluded (Boyle *et al.,* 1995), it is thought the data collected can reflect changes in population biology or between-year variability in seasonality and recruitment. A spatial length frequency analysis was therefore carried out on survey data.

Holme (1974) reported that the main spawning season of *L. forbesi* in the English Channel occurs in offshore grounds, and Lordan and Casey (1999) described the appearance of Irish *L. forbesi* egg masses in offshore areas suggesting that spawning should occur in these distant from coast areas. Taking into account these suggestions and the life cycle described by Collins *et al.* (1997), the occurrence of the higher length class (C6) or smaller length class (C2) in winter and summer, was expected in offshore areas, while the length class 4 (C4) was expected in inshore waters during autumn and spring, because full recruitment to the fishery occurs at a mantle length of approximately 15cm (Pierce *et al.,* 1994*b*). However such a clear pattern it is not detectable and squid of length classes C4 and C6 do not reveal any consistent distribution pattern apart from their disappearance from offshore waters in August and in some years in March. Squid from C2 seem to be close to shore in August and December, also appearing far from the coast in some years and seasons. This analysis seems not to contradict the above suggestion that summer breeders spawn inshore, since all length classes appear only in inshore waters. In support of this suggestion some egg masses from static fishing gear where found in these areas around Ireland (Collins *et al.,* 1995) and Scotland (Lum-Kong *et al.,* 1992). The suggestion that autumn recruits recruit inshore is also supported, again because during these seasons small and big animals only appear inshore.

Length frequency analysis on veined squid survey data can experience some interference. The presence of two cohorts, or microcohorts together in the same dataset, as described by (Pierce *et al.* ,2005) and also found for example in the squid *Sepioteuthis australis* (Moltschaniwckyj and Pecl, 2007), can lead to a misinterpretation of *L. forbesi* movements and their relationship with their life cycle, since more than one maturity stage is present in the analysis, and because the incorrect identification of *Allotheutis sp.*, sometimes confused for small *L. forbesi* (Pierce *et al*., 1994), could incorrectly suggest the presence of small *L. forbei*. In addition to these complications, it has been argued that some of the apparent variability in seasonality of the life cycle of *L. forbesi* reflects variation in the relative strength of summer and winter breeding populations (Zuur and Pierce, 2004).

4.3. Environmental analysis and statistics

4.3.a. Migratory behaviour is a characteristic feature of some squid (Hanlon and Messenger, 1996). During their ontogenesis, squid undertake horizontal and vertical migrations to the regions with optimal environmental conditions for spawning, egg development, and juvenile and adult growth (ontogenetic migrations) (Nesis, 1985). Several studies have been carried out in order to understand in which way the environmental conditions affect squid species' migrations, movements and distribution, in particular the effect of sea surface temperature (SST) (Arkhipkin *et al.,* 2004). In the present study, GAMM was the chosen approach to find and understand the relationships between environmental conditions and *L. forbesi* distribution during the different stages of their life cycle. In both datasets used, the response variable was length, either (A) treating each length class of each haul as a data point or (B) using the average length of all squid in a haul as a data point. The third option, of treating the length of each individual squid as a datapoint, was rejected: since squid move in shoals, individuals of the same length class in the same haul cannot be considered to be independent samples and treating them as such would artificially inflate degrees of freedom (i.e. it would be pseudo-replication). On the other hand, using the overall average per haul undoubtedly disguises real complexity in the length-frequency data and option A was also selected, as the best compromise.

In analyses of both datasets, distance of the haul to coast is the most significant parameter, in almost all seasons, which can indicate the presence of an important inshore-offshore movement (or, at least, segregation by size). The main trends visible in the smoothers representing the effect of distance to coast were as follows: there was a more important effect of distance in the first 80miles from the shore, meaning that, within this area, the effect of proximity to coast on observed body size is very significant. In winter and spring an inverse relationship between length class and distance to coast seems to exist, in that bigger squid tend to be closer to the coast than small squid, whereas in summer the relationship seems to be the opposite, with immature squid appearing in more coastal waters than mature squid (although in summer distance to coast is not the most significant explanatory variable). As documented for *L. pealeii* (Hatfield and Cadrin, 2001), these trends can indicate a migration from offshore to inshore grounds of squid about to recruit during spring. Therefore, the summer cohort is likely to spawn inshore, as suggested by results from abundance and length frequency analysis, since spring recruiters seem to disappear from offshore grounds. *L. forbesi* in the English Channel spawns during winter in offshore grounds (Holme, 1974), and according to these GAMM analyses, Scottish *L. forbesi* might also spawn in offshore areas during winter, although this suggestion is not supported by any other analysis performed in the present study, but is also not in disagreement. However, uncertainty remains because the smoothing curves for the effect of distance in summer and autumn are difficult to interpret - and in model B the effect of distance was not significant in summer.

During summer months, depth and SST seem to be the most significant variables, with very similar *p*-values. During this season *L. forbesi* length increases with depth and SST, although from 250m depth the effect is no longer positive, and above 12°C there is no trend. A similar pattern was observed by Sacau *et al.* (2005) in *Illex argentinus*, for which GAM analysis revealed higher abundances and maturity appearing in the warmer and deeper waters of the southwest Atlantic. Therefore in these (summer) months, veined squid seem to move depending on the SST and depth. In spring, apart from distance to coast, SST and especially depth are also highly significant explanatory variables. Depth seems to have a defined influence on size distribution between 100 and 250m, down to ~175m squid length decreases but in deeper waters the relation is inverse, showing a peak of small squid at this depth. Where SST smoother have effect, above 8 °C, it seems that the trend is linear, size is equally distributed within all temperature range, which is in accordance with results the from studies by Pierce *et al.* (1998) and Waluda and Pierce (1998) that suggest that *L. forbesi* in the North Sea occurs in regions with warm water inflows and avoid regions with water temperatures below 7°C.

Although the positive effect of depth appears only between 75 and 250m and is not the most significant effect in all seasons, there is a trend: small squid prefer shallower water and bigger squids prefer deeper water, just as Arkhipkin *et al.* (2004*a*) argued for *L. gahi* from the Falkland Islands where body size generally increases with depth in all seasons.

In general the effect of SST is positive above 8°C, but the way it influences *L. forbesi* size distribution is different between seasons. In summer and spring the squid from all sizes are equally distributed within temperature range, although in summer is possible to exist a peak of size at 11°C. In autumn and winter, temperature has opposite effects on squid distribution; in autumn smaller squid seem to appear in colder waters and in winter they are in warmer waters. This can indicate that the winter cohort searches for colder waters to spawn once in their breeding season, bigger therefore more mature squid, appear in colder waters but they recruit and feed in warmer water since in their most documented recruitment season, Autumn (Collins *et al.,* 1997, 1999; Pierce *et al.,* 1998, 2001), bigger squid appear in warmer waters. However SST variation is very small and in these two seasons, SST has a significant effect only in model A and even then is not the most important explanatory variable.

The results from GAMM in A and B seem very similar and therefore, since both models provide a good fit to the data, this is considered to be representative of what is happening in nature to *L. forbesi* size distribution. However, both data sets have advantages and disadvantages: model A might have a good observation number but does not take into account the frequency of each length class in the haul, i.e. one hundred squid have the same influence in the model as one, which can lead to wider confidence bands. On the other hand, this approach separates each length class found in each haul allowing for better results in discovering the links between size and environmental conditions, an advantage not shared with model B. In this second model, in addition to the small number of observations, the combination of all length classes of each haul constitutes a disadvantage, but by doing this we can decrease the influence of discarding frequency of squid in each haul. These disadvantages might explain why some of the smoother curves are not clearly interpretable and the lower number of observations in model B can be a reason for the less significant smoothers when comparing with model A.

4.3.b. With the analyse of GAMM from survey data, we can infer that SST and depth are not the most important environmental variables influencing *L. forbesi* size distribution but it is probable they influence abundance as suggested in previous studies (i.e Pierce *et al.,* 1998; Waluda and Pierce 1998; Bellido *et al.,* 2001; Sims *et al.,* 2001), especially in winter seasons. It has been recently shown that fluctuations in the abundance of squid species, e.g. *L. gahi* and *Illex argentinus*, may depend on environmental conditions, mainly SST, on their spawning grounds (Arkhipkin and Middleton, 2002).

In the present study, the presence/absence and abundance-given-presence model on fishery data, using GAMM approach, shows that all explanatory variables are equally significant to determine squid abundance and distribution in almost all months. Therefore for a predictive model distance to coast, bathymetry and SST must be considered, as suspected from the previous GAMM size model, since all explanatory variables are also significant even if with different values. The presence/absence model, previously used by Pierce *et al.* (1998) to model *L. forbesi* abundance distribution using regression trees techniques, reveals what is confirmed by the model of abundance–given-presence data, the abundance decreases with the distance to coast and increases with depth and SST until ~10°C, above which temperatures squid abundance decreases with temperature. This suggests that environmental conditions can probably lead *L. forbesi* to move in search for their optimal environment found in waters closer from coast when SST is around 10°C and at 200m depth, as reported for *L. gahi* from the Falkland Islands (Arkhipkin *et al.,* 2004). However, taking into account the previous GAMM analysis using size class as response variable, we can suggest that these influences on abundance and distribution might depend on the maturation stage. Therefore, if for example a fishery is to take place in autumn (November/December), a haul at 200m depth and in warm waters about 10°C, would not only be more successful in terms of catch rate but probably would result in a catch of bigger *L. forbesi* than in shallower and cooler waters.

Due to the similarity of the significance values of the smooth terms it is not possible to detect which variable is most important to determine abundance, as we can for size class. Therefore it seems that the choice of place to complete the life cycle inshore or offshore, are made according to the environmental conditions.

5. Conclusions and Future work

The application of traditional and new technologies, such as GIS and length frequency analysis, revealed a coast to coast non-migratory behaviour of Scottish *L. forbesi*, in opposition to what was previously suggested by Waluda and Pierce (1998), however an inshore/offshore movement seem to be present in agreement with what was reported for other squid species such as *L. gahi* (Arkhipkin *et al.,* 2004*a*) and *L. paelli* (Hatfield and

Cadrin, 2001). In spring and summer veined squid appear mostly in inshore waters, which reveal that the summer cohort spawns inshore as well as the spring recruitment. During autumn and winter squid start to appear in offshore waters but never disappear from inshore grounds. However, although these patterns seem consistent, several issues such as where winter breeder spawn and spring recruitment occurs remain, therefore to complete this study or to implement a management technique a more complete survey data collection, aging techniques (e.g. using statoliths) and/or cohort analysis are necessary to separate the two possible cohorts in order to detect the precise migration movements of each cohort. In addition, the extension of the genetic analysis of Shaw *et al.* (1999) can also be helpful with to determine for example if the two cohorts have different migratory behaviours, if they belong to same population or to other such as from Rockall banks, where they would spent part of the life cycle and migrate into more coastal areas in some months.

However before answering these important questions, a fundamental issue is still uncertain: what is exactly the life cycle of *L. forbesi*? It seems that the presence of two cohorts is unanimously agreed between authors but whether they complete the life-cycle in one year or more is not clear, which hinders studies that require this knowledge. Spawning and recruitment seasons, and their duration, remain still to understand and common techniques, such as length frequency analysis, are affected by this uncertainty and therefore the veracity of the results can also be unclear.

To determine the apparent inshore-offshore movements of *L. forbesi* in Scottish waters, a tagging program could be helpful just as Lipinski *et al.* (1998) and Sauer *et al.* (2000) did with success for chokka squid in South Africa. Diet studies are also a possible approach since it is known that predators also move according to their prey or to avoid their own predators, studies regarding prey distribution and stomach contents of eventual predators such as marine mammals or birds and big pelagic fish as Lansdell and Young (2007) did successfully when analysing swordfish and yellowfin tuna samples in Australian waters, can help to identify more possible movements and their reasons. Hydroacoustic methods are also a possibility to infer *L. forbesi* migration movements as Lipinski and Soule (2007) suggested for chokka squid in South Africa.

During summer *L. forbesi* size distribution is mostly influenced by depth and sea surface temperature, however during the remainder of the year, temperature seems to become less important and distance to coast becomes the most important variable in squid size distribution. Abundance distribution on the other hand seems equally dependent on all the studied environmental conditions: body size and abundance generally increase with depth and decrease with distance to coast. *L. forbesi* therefore seems to have their optimal environmental conditions in inshore waters (~25 miles from coast) at around 10°C and with a bathymetry of 200m although these conditions can vary according to maturity stage.

6. References

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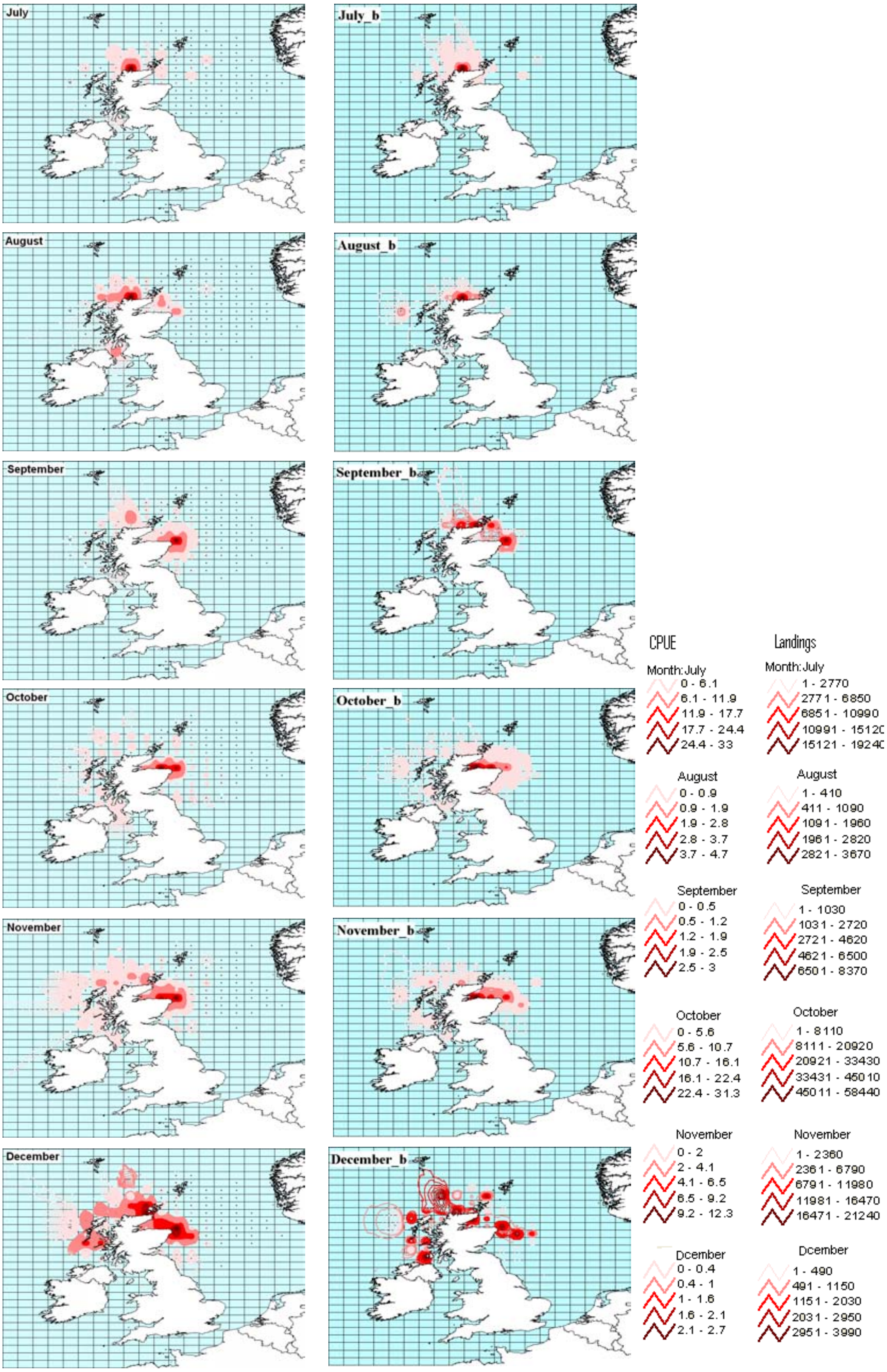
Appendix I – Annual GIS maps comparing CPUE and landings as abundance index



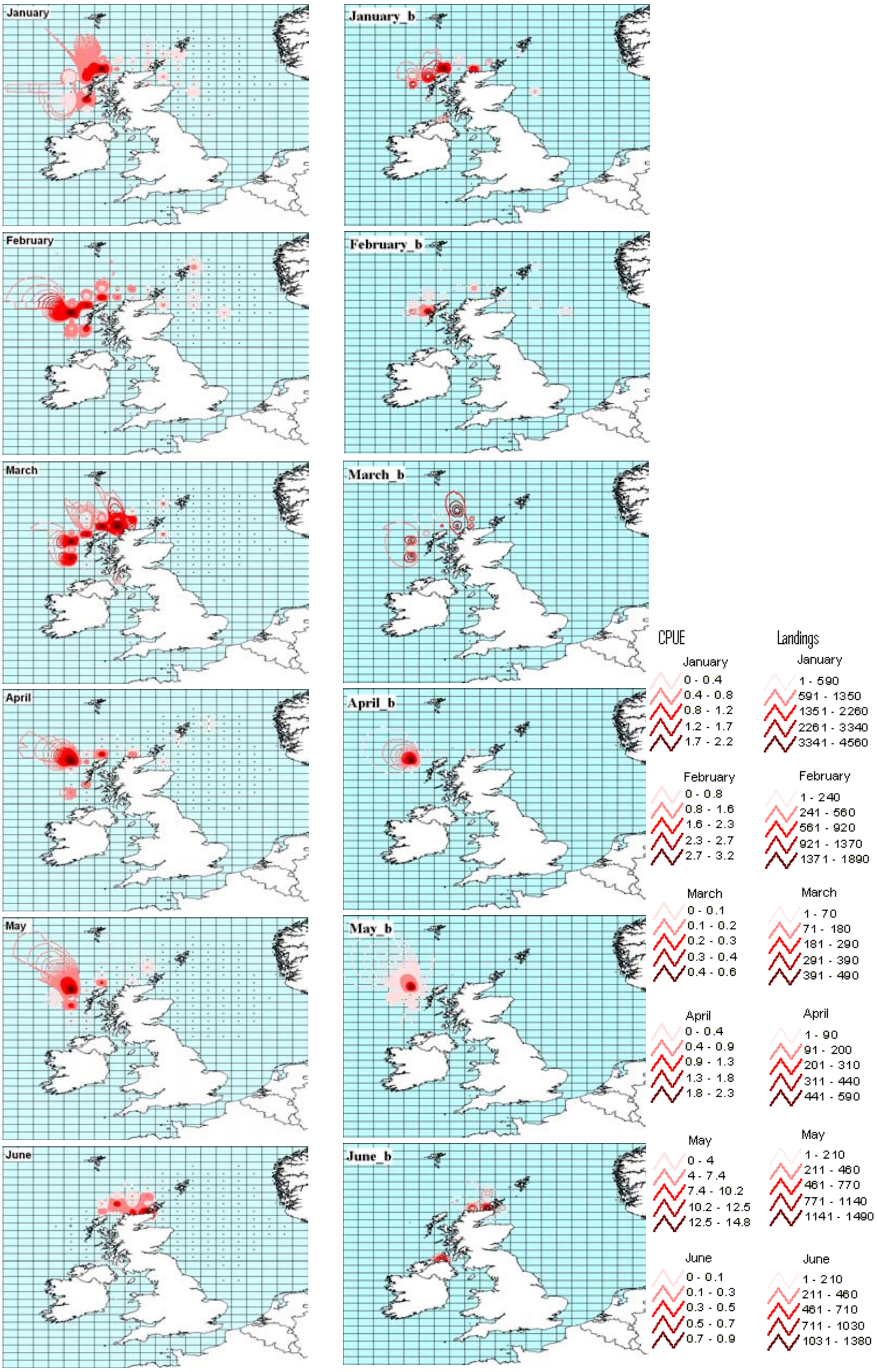
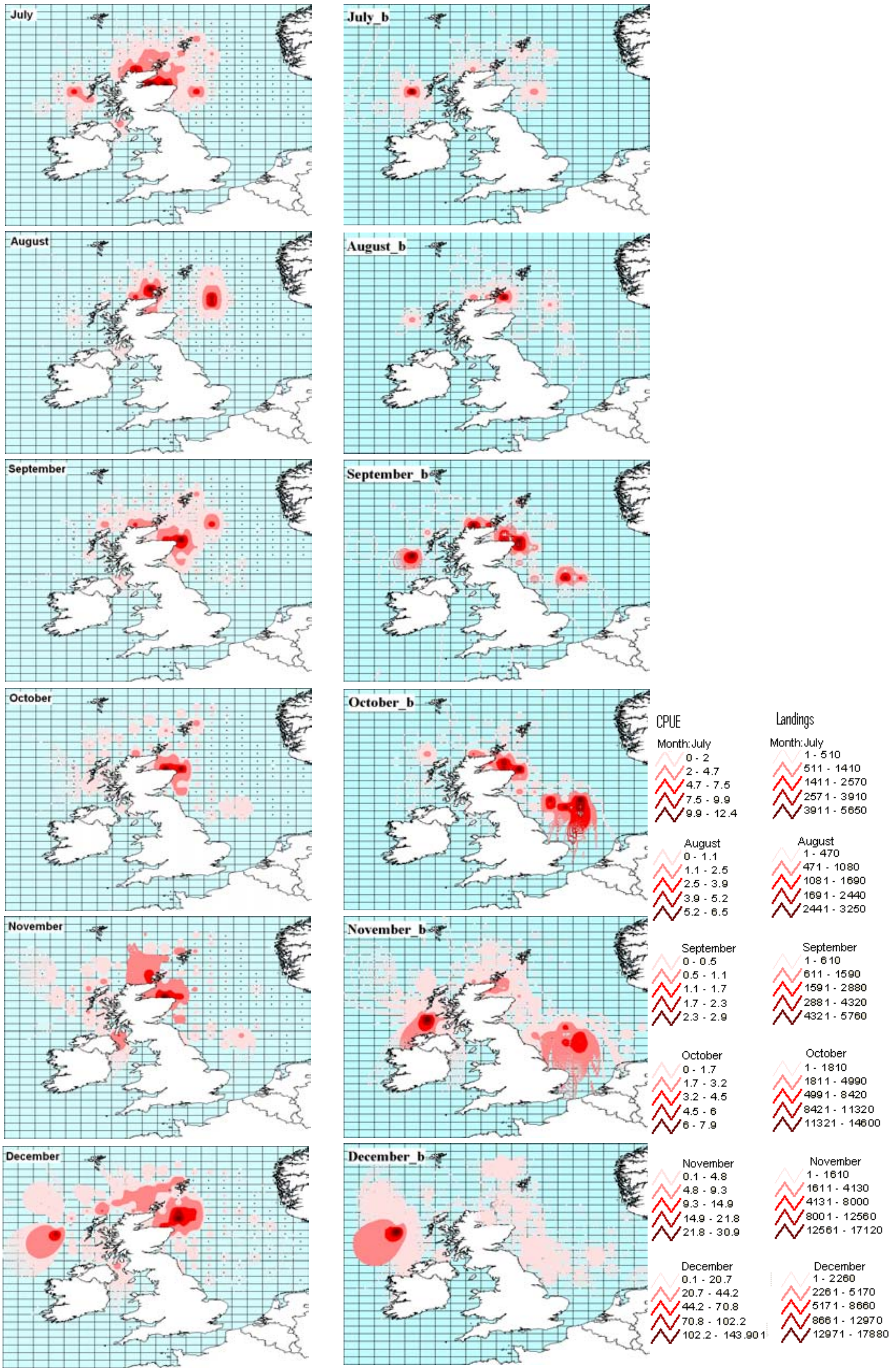


Fig. 1 – Maps showing *Loligo forbesi* abundance distribution from July of 1984 to June of 1985, in Scottish waters, achieved from landings in Kg (left) and CPUE in Kg per hour of effort (right, b).


July
July_b
August
August_b
September
September_b
October
October_b
November
November_b
December
December_b
CPUE
Month: July
0 - 2
2 - 4.7
4.7 - 7.5
7.5 - 9.9
9.9 - 12.4
August
0 - 1.1
1.1 - 2.5
2.5 - 3.9
3.9 - 5.2
5.2 - 6.5
September
0 - 0.5
0.5 - 1.1
1.1 - 1.7
1.7 - 2.3
2.3 - 2.9
October
0 - 1.7
1.7 - 3.2
3.2 - 4.5
4.5 - 6
6 - 7.9
November
0.1 - 4.8
4.8 - 9.3
9.3 - 14.9
14.9 - 21.8
21.8 - 30.9
December
0.1 - 20.7
20.7 - 44.2
44.2 - 70.8
70.8 - 102.2
102.2 - 143.901
Landings
Month: July
1 - 510
511 - 1410
1411 - 2570
2571 - 3910
3911 - 5650
August
1 - 470
471 - 1080
1081 - 1690
1691 - 2440
2441 - 3250
September
1 - 610
611 - 1590
1591 - 2880
2881 - 4320
4321 - 5760
October
1 - 1810
1811 - 4990
4991 - 8420
8421 - 11320
11321 - 14600
November
1 - 1610
1611 - 4130
4131 - 8000
8001 - 12560
12561 - 17120
December
1 - 2260
2261 - 5170
5171 - 8660
8661 - 12970
12971 - 17880

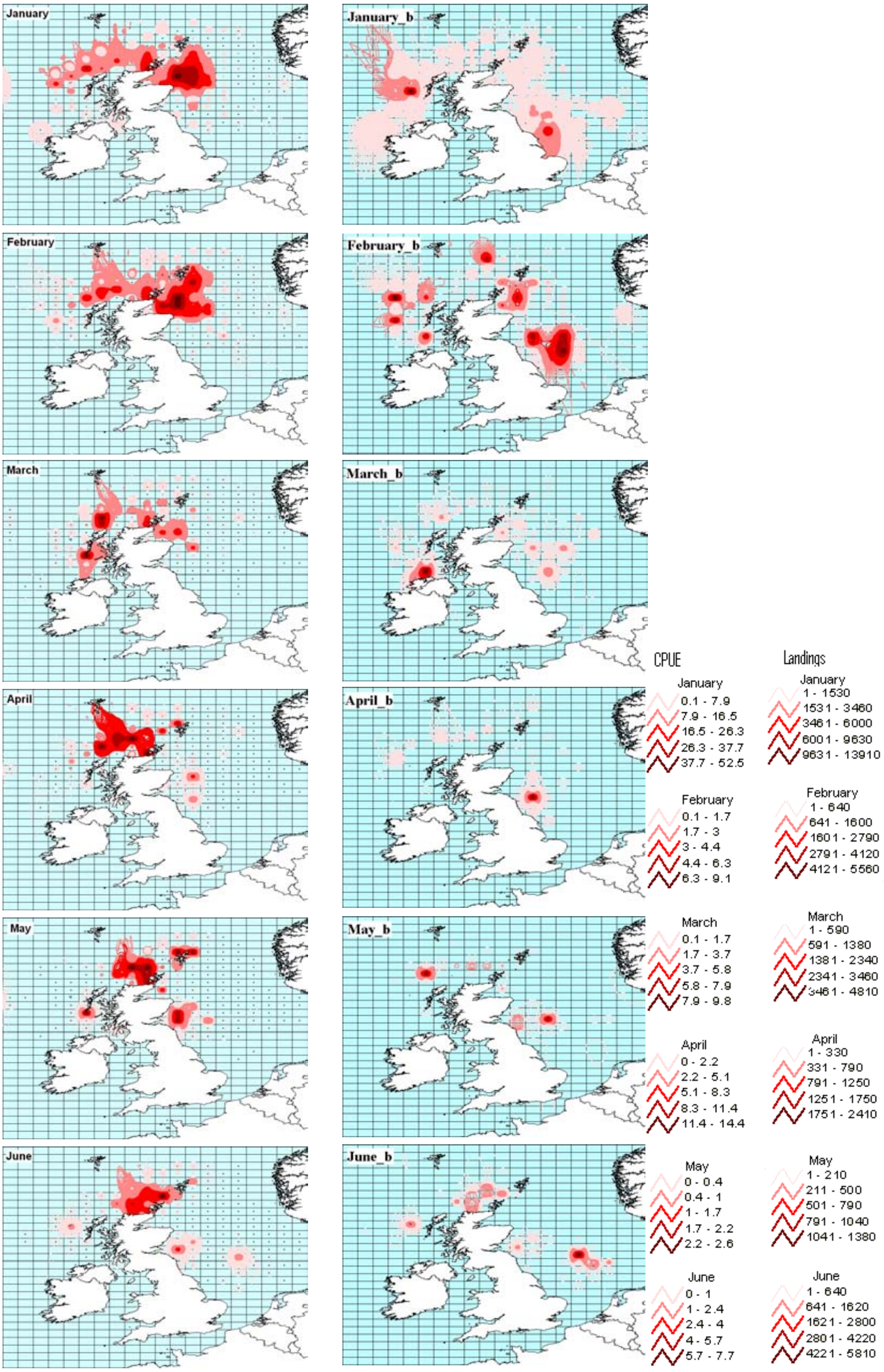


Fig. 2 – Maps showing *Loligo forbesi* abundance distribution from July of 1997 to June of 1998, in Scottish waters, achieved from landings in Kg (left) and CPUE in Kg per hour of effort (right, b).

Appendix II – Comparison of three models: GAM, GAMM and GAMM with year as random effect; and three different survey dataset.

Table I – Approximate significance values and AIC of the smooth terms distance to coast, depth and sea surface temperature (SST) where the haul was performed obtained with three different approaches, GAM, GAMM and GAMM with year as a random effect, and three different data set. In all data set length is the response variable but in Lclass the different length classes caught in each haul is considered a datapoint, in Squid each squid caught is an independent datapoint and in haul x is the average length class of the all squid caught in each haul. Data used are from 1982 to 1992 except for Haul dataset that uses comprehends data until 2004.

	GAM			**GAMM Random**			**GAMM**		
	Lclass	**Squid**	**Haul**	**Lclass**	**Squid**	**Haul**	**Lclass**	**Squid**	**Haul**
Dist.	0.168	4.4e-06	0.291	0.066	0.116	0.069	0.046	0.342	0.154
Depth	0.007	2e-16	2.6e-05	0.000	2.2e-16	6.6e-06	0.001	2e-16	3.8e-05
SST	5.9e-06	2e-16	2.8e-07	0.028	2.3e-13	5.5e-07	0.010	2e-16	2.6e-07
Df Dist.	5.023	8.791	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Df depth	3.501	4.142	8.058	4.619	6.806	4.313	4.425	6.644	3.757
Df SST	8.765	8.914	7.031	1.000	6.472	6.433	1.000	8.131	6.811
AIC				1063	4410	1329	1062	4410	1337

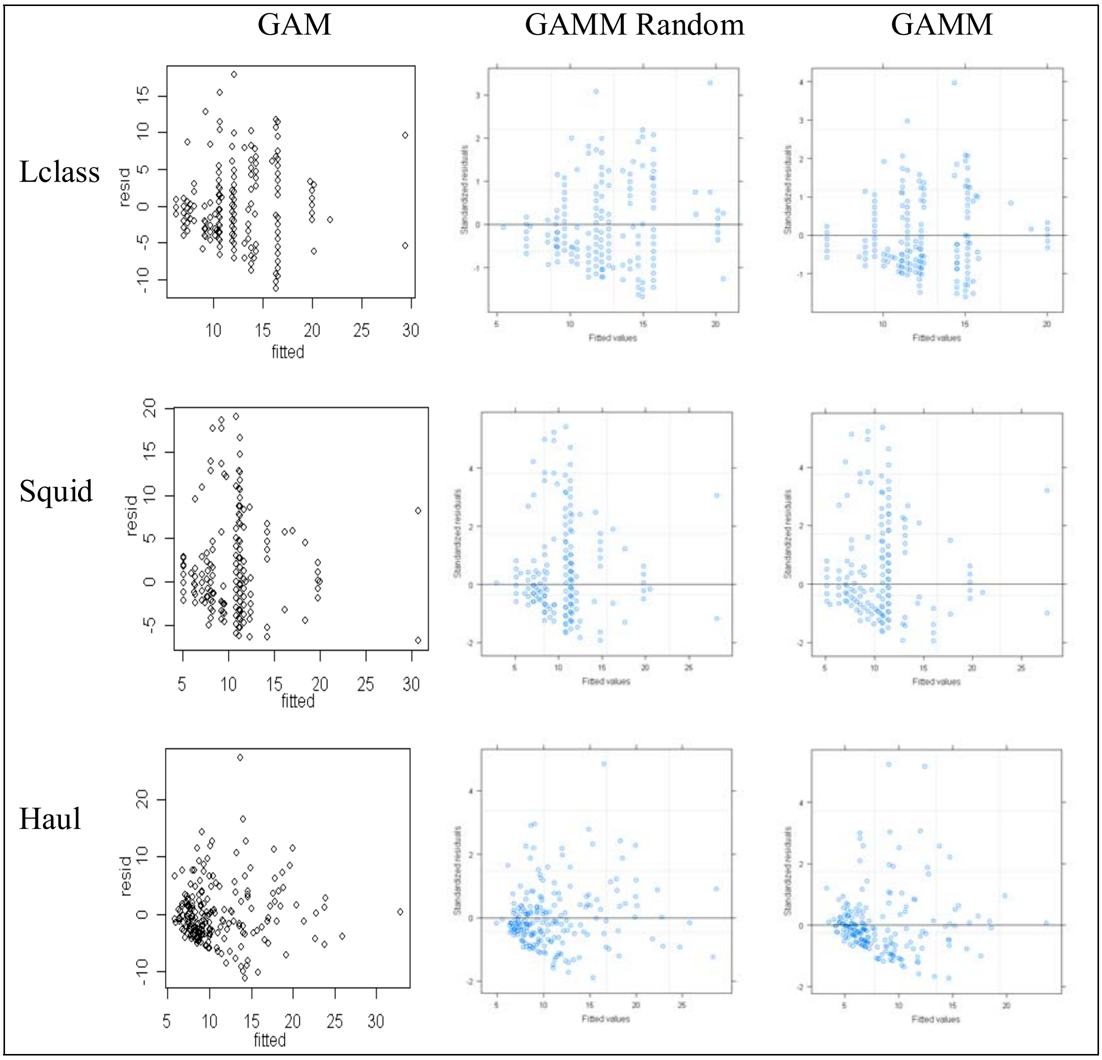


Fig 1 – Residuals against fitted values of three different models, GAM, GAMM and GAMM with year as random effect. Each models was performed for three data sets with length as response variable. However in Lclass x is the different length classes caught in each haul, in Squid each squid caught is an independent sample and in haul x is the average length class of the squid caught in each haul.

Appendix III – Annual GIS abundance maps

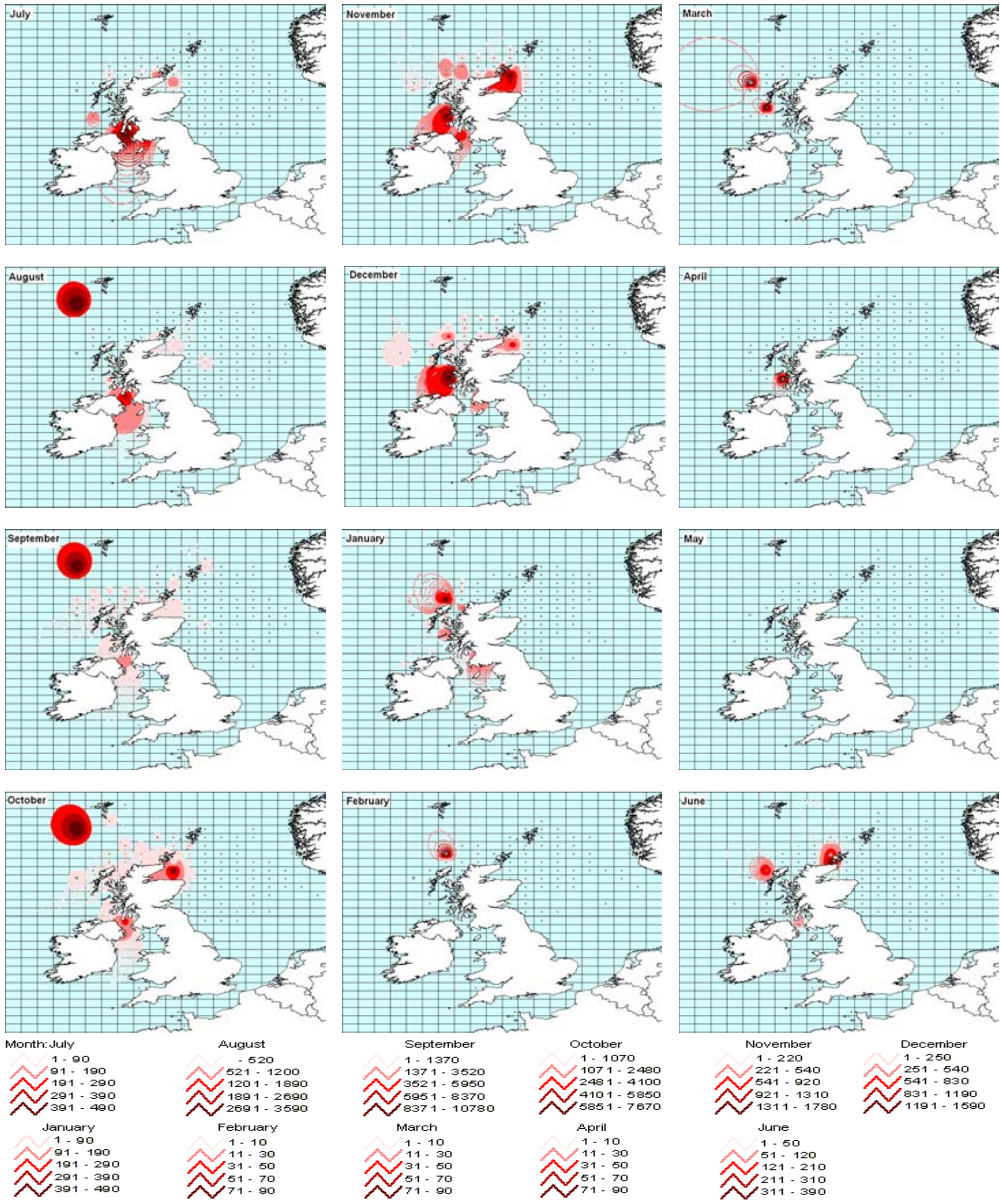


Fig. 1 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1980 until June of the following year, 1981. Black dots represent the presence of haul(s) in the ICES square.

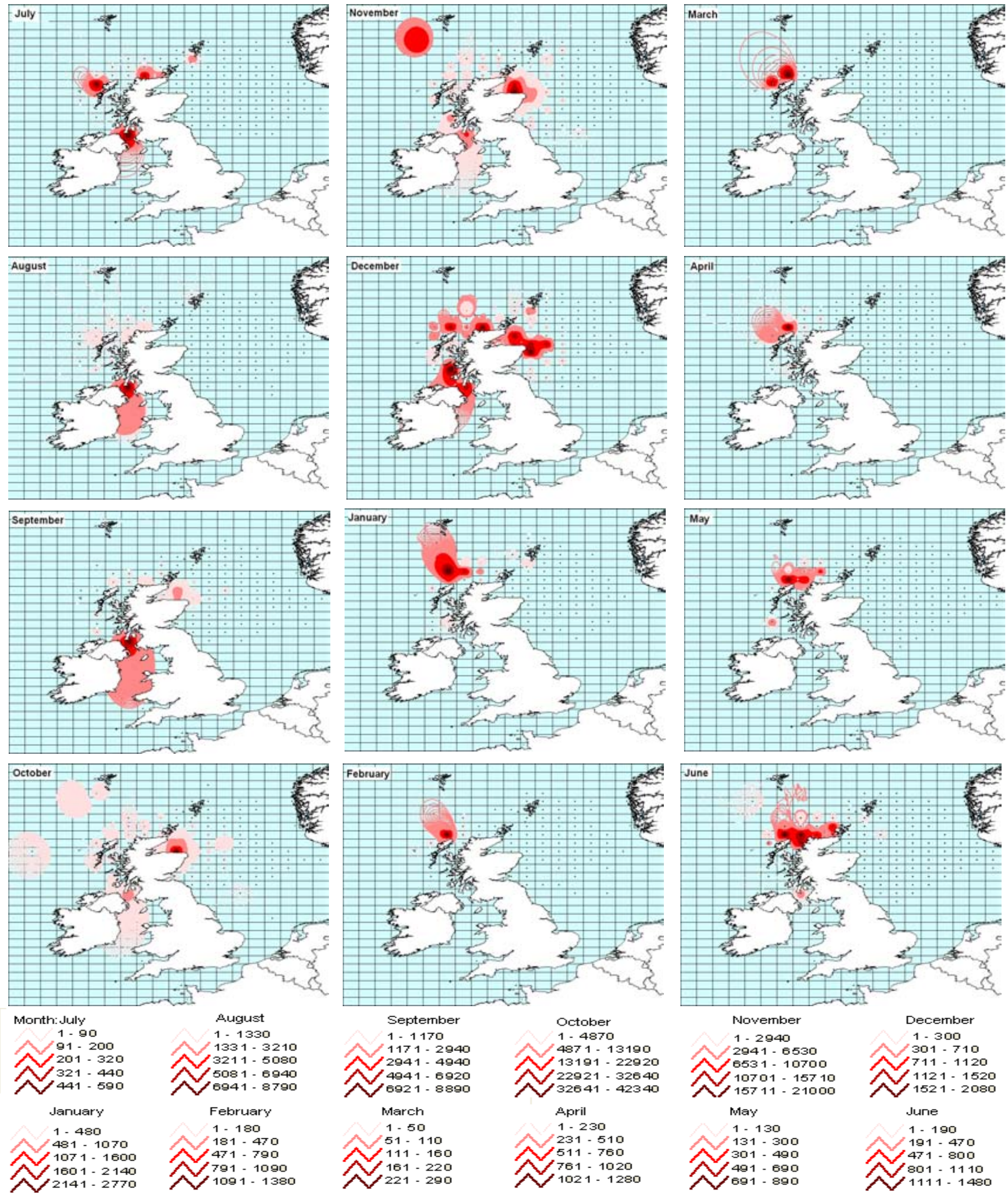


Fig. 2 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1981 until June of the following year, 1982. Black dots represent the presence of haul(s) in the ICES square.

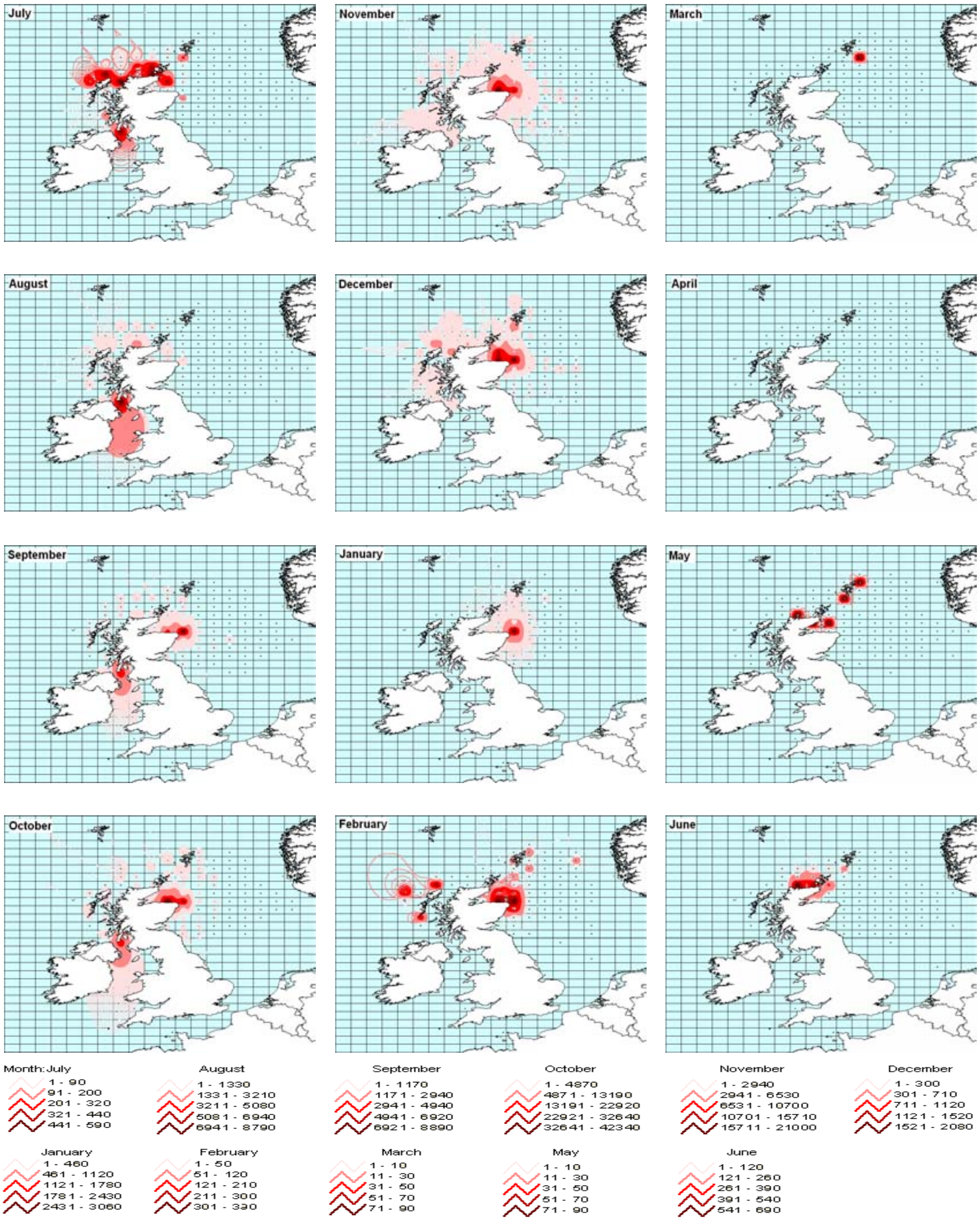


Fig. 3 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1982 until June of the following year, 1983. Black dots represent the presence of haul(s) in the ICES square.

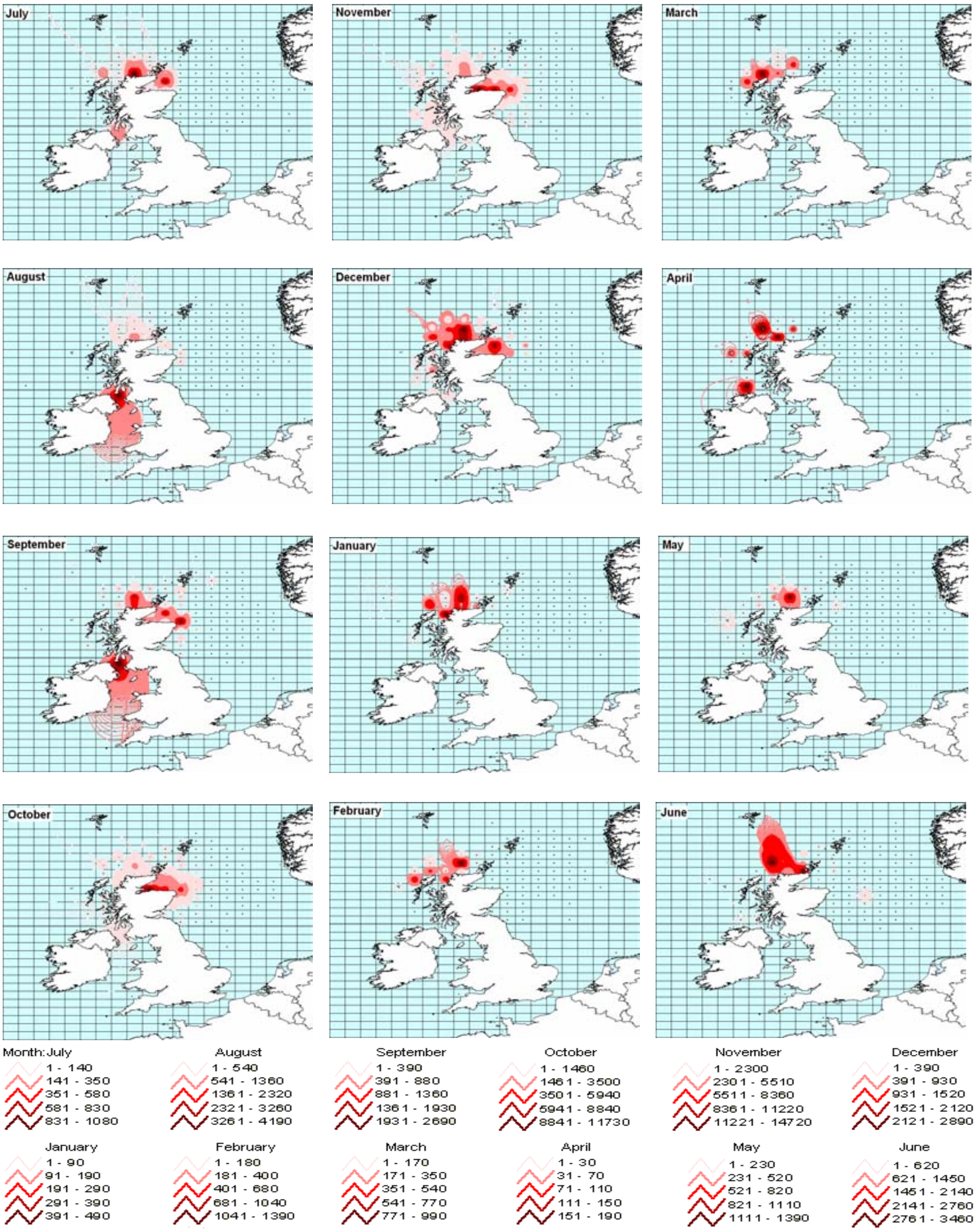


Fig. 4 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1983 until June of the following year, 1984. Black dots represent the presence of haul(s) in the ICES square.

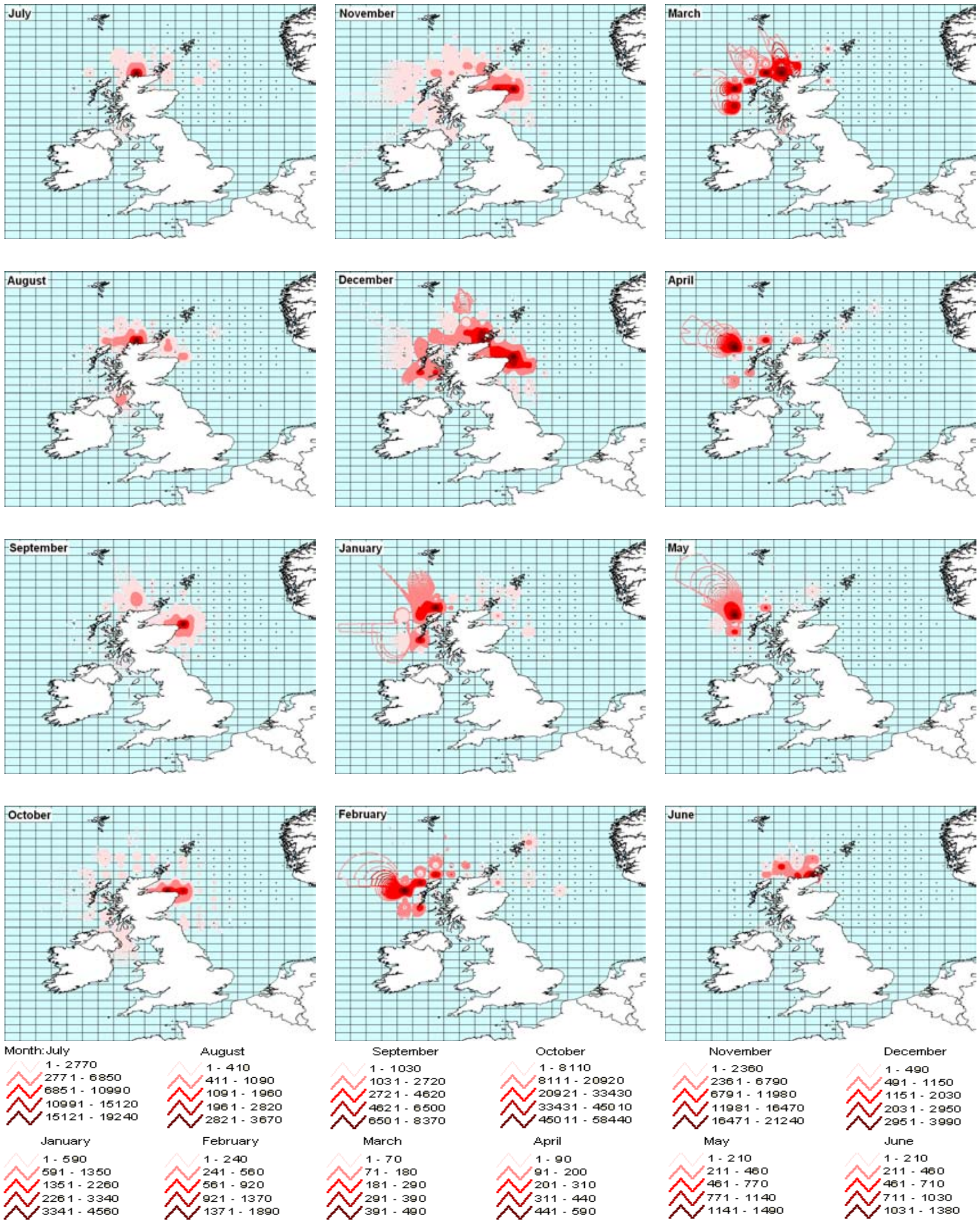


Fig. 5 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1984 until June of the following year, 1985. Black dots represent the presence of haul(s) in the ICES square.

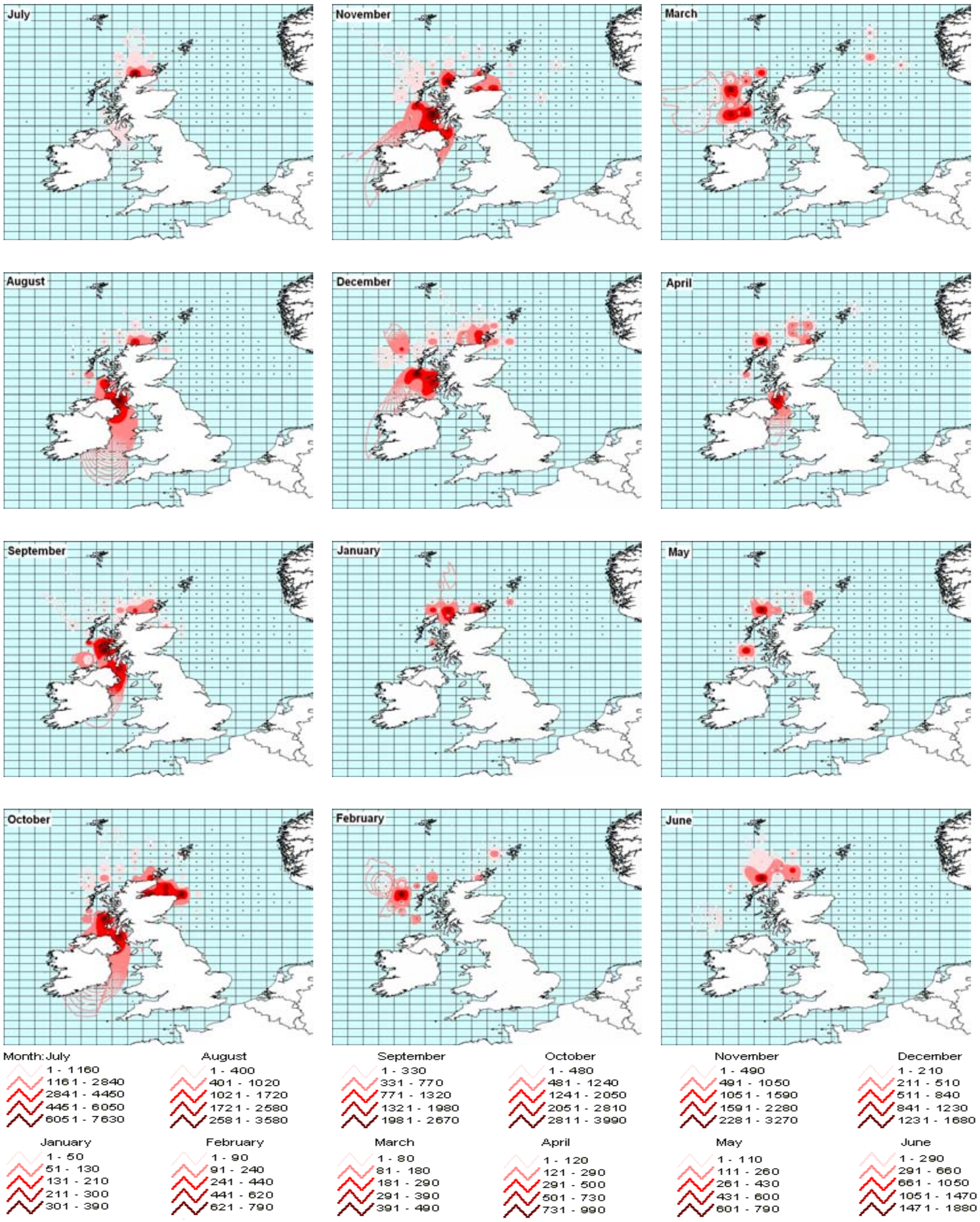


Fig. 6 – Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1985 until June of the following year, 1986Black dots represent the presence of haul(s) in the ICES square.

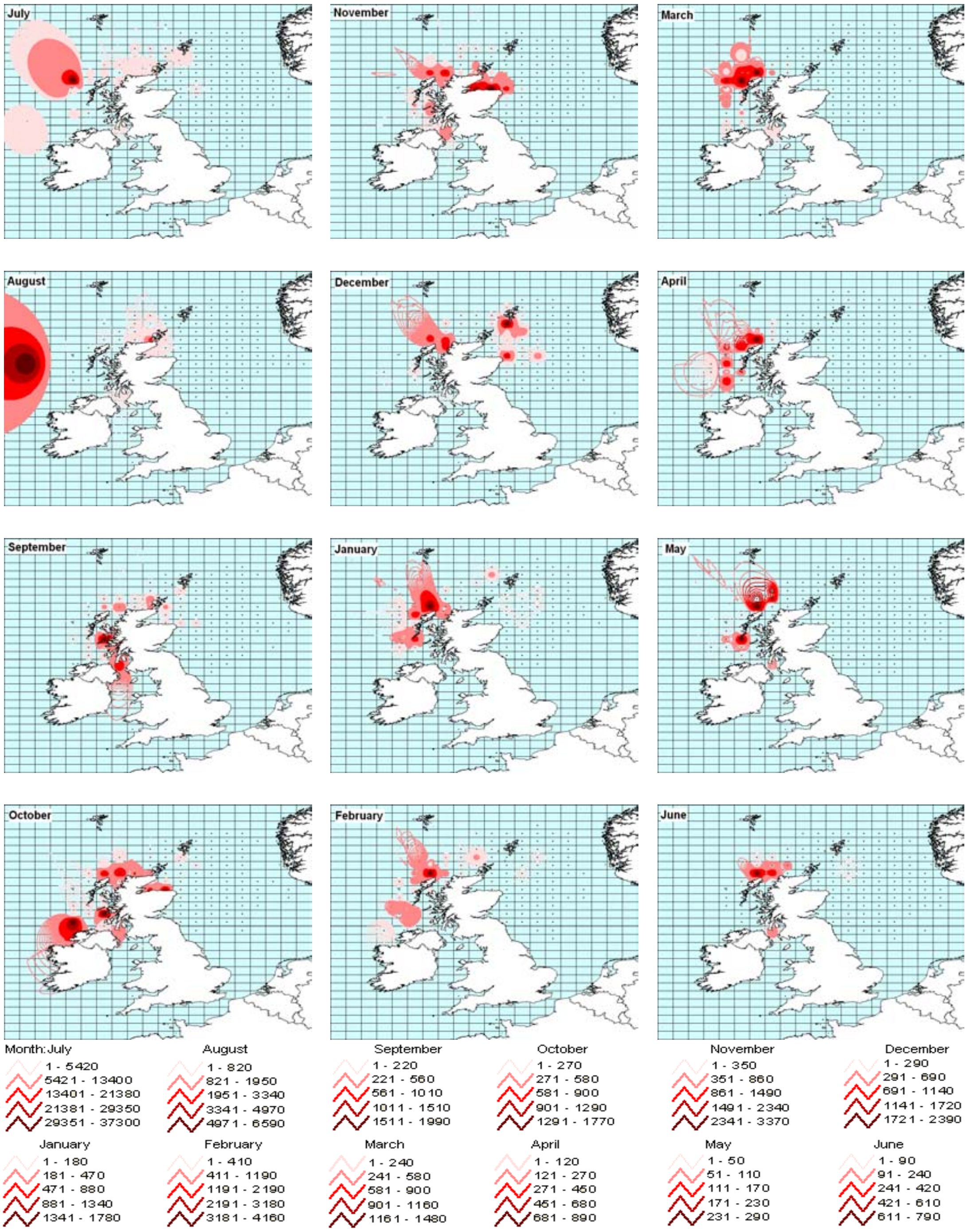


Fig. 7 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1986 until June of the following year, 1987. Black dots represent the presence of haul(s) in the ICES square.

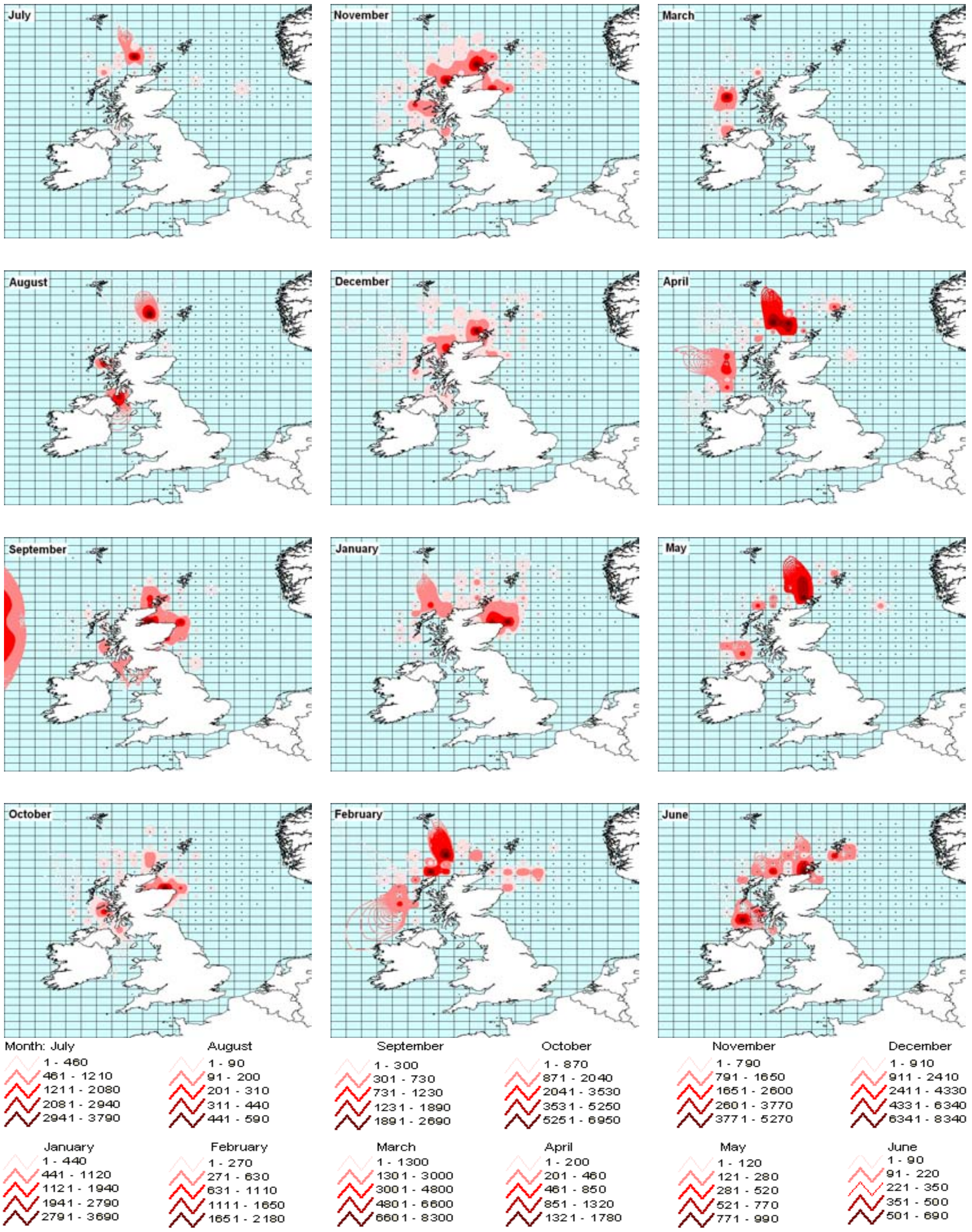


Fig. 8 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1987 until June of the following year, 1988. Black dots represent the presence of haul(s) in the ICES square.

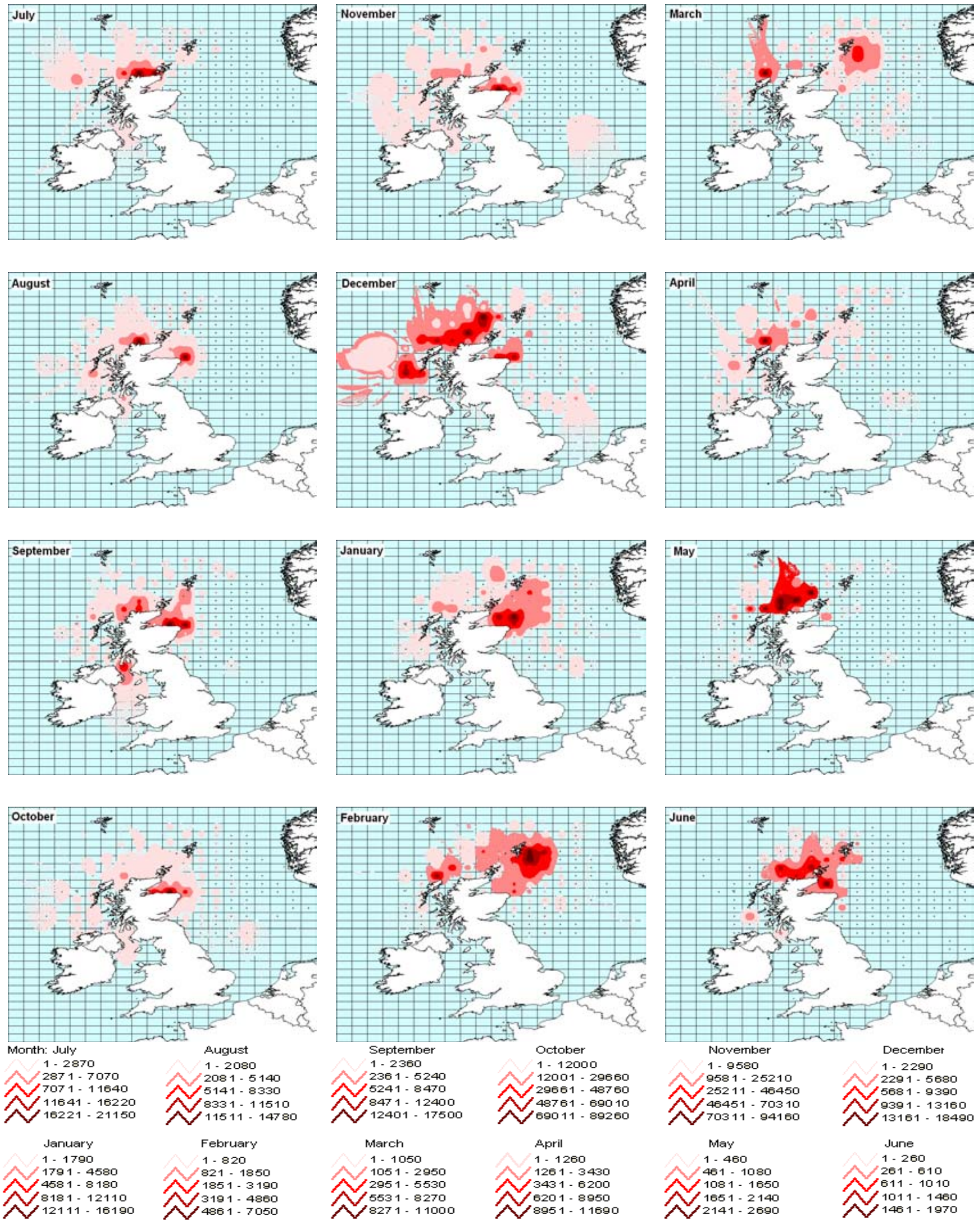


Fig. 9 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1989 until June of the following year, 1990. Black dots represent the presence of haul(s) in the ICES square.

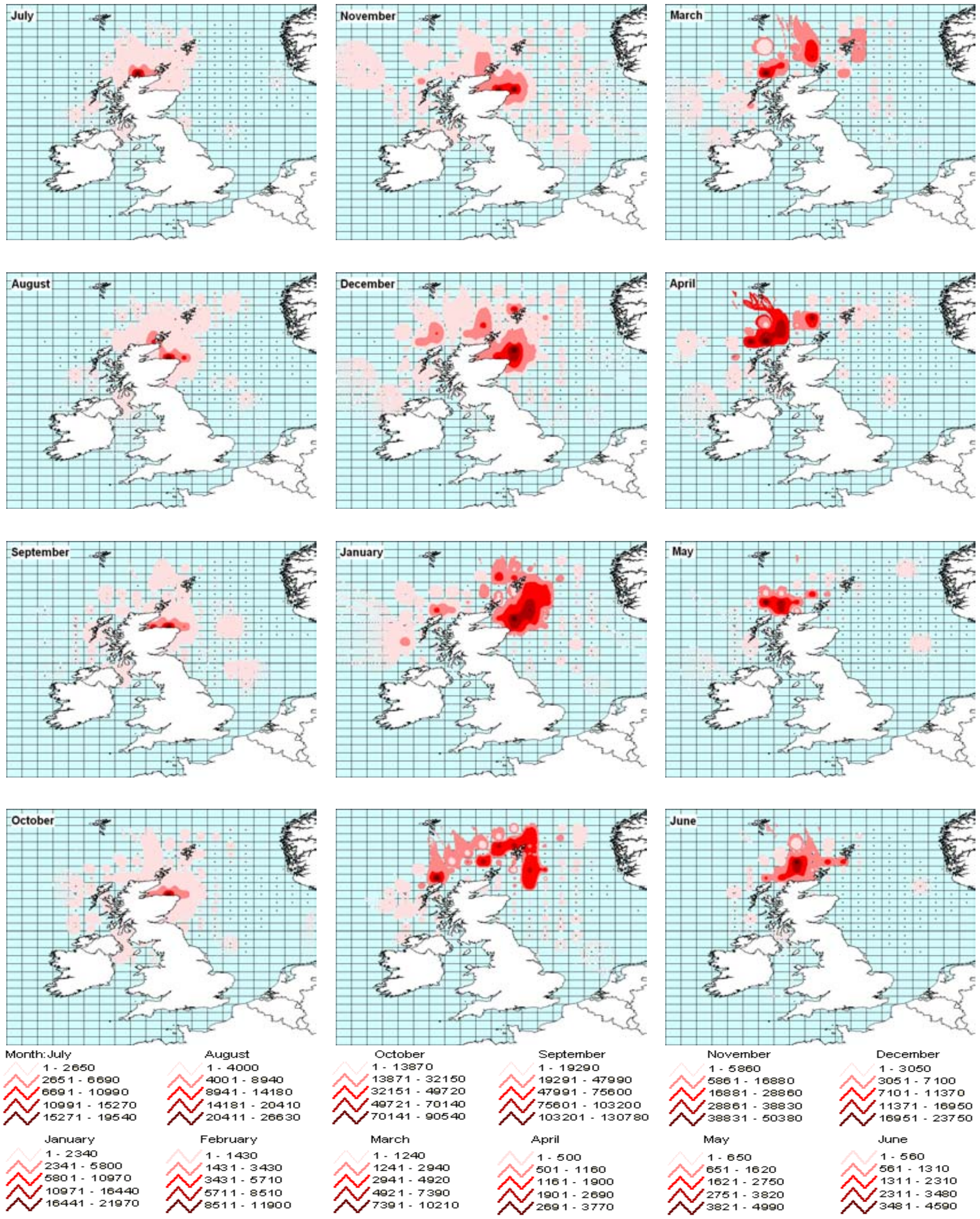


Fig. 10 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1990 until June of the following year, 1991. Black dots represent the presence of haul(s) in the ICES square.

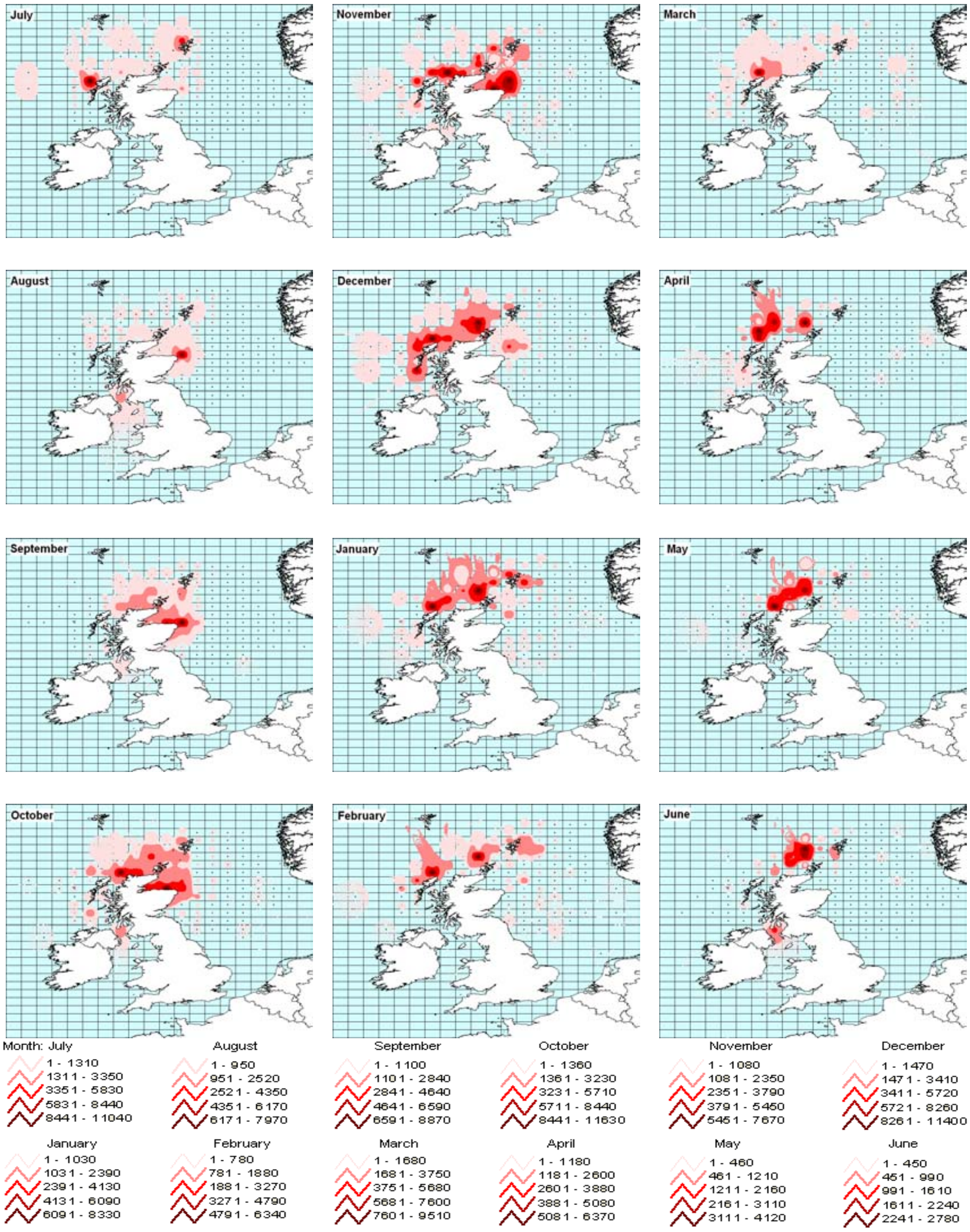


Fig. 11 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1991 until June of the following year, 1992. Black dots represent the presence of haul(s) in the ICES square.

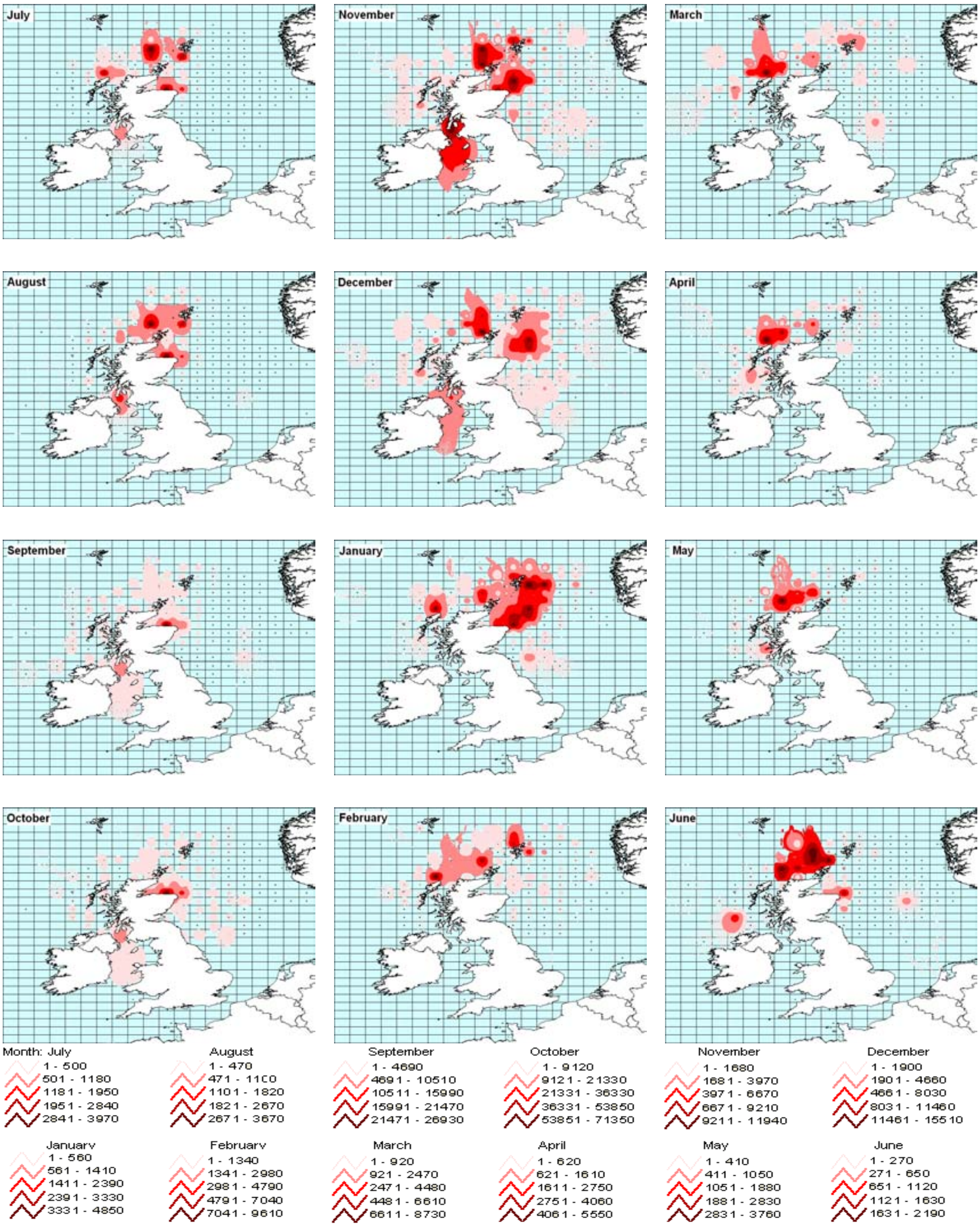


Fig. 12 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1992 until June of the following year, 1993. Black dots represent the presence of haul(s) in the ICES square.

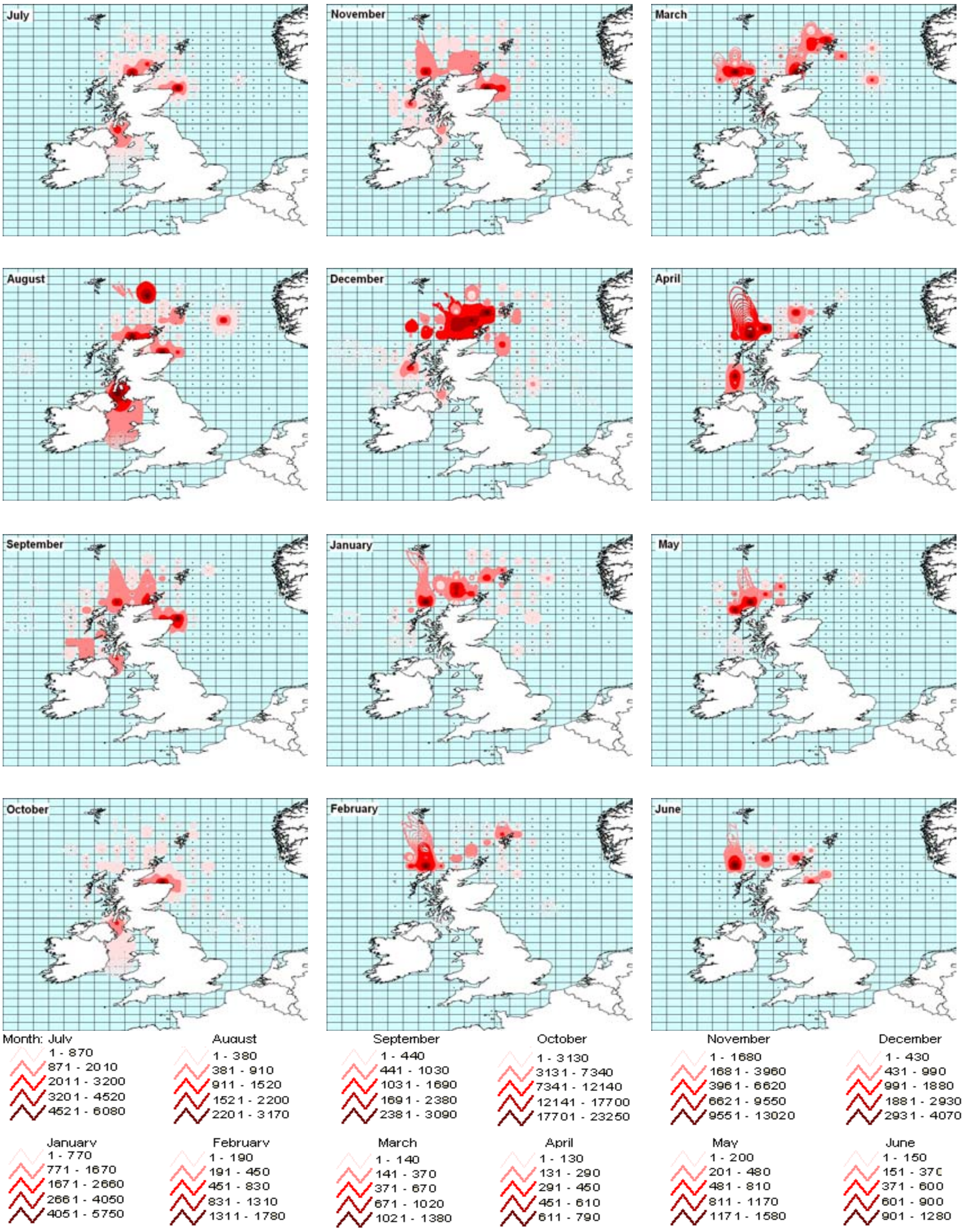


Fig. 13 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1993 until June of the following year, 1994. Black dots represent the presence of haul(s) in the ICES square.

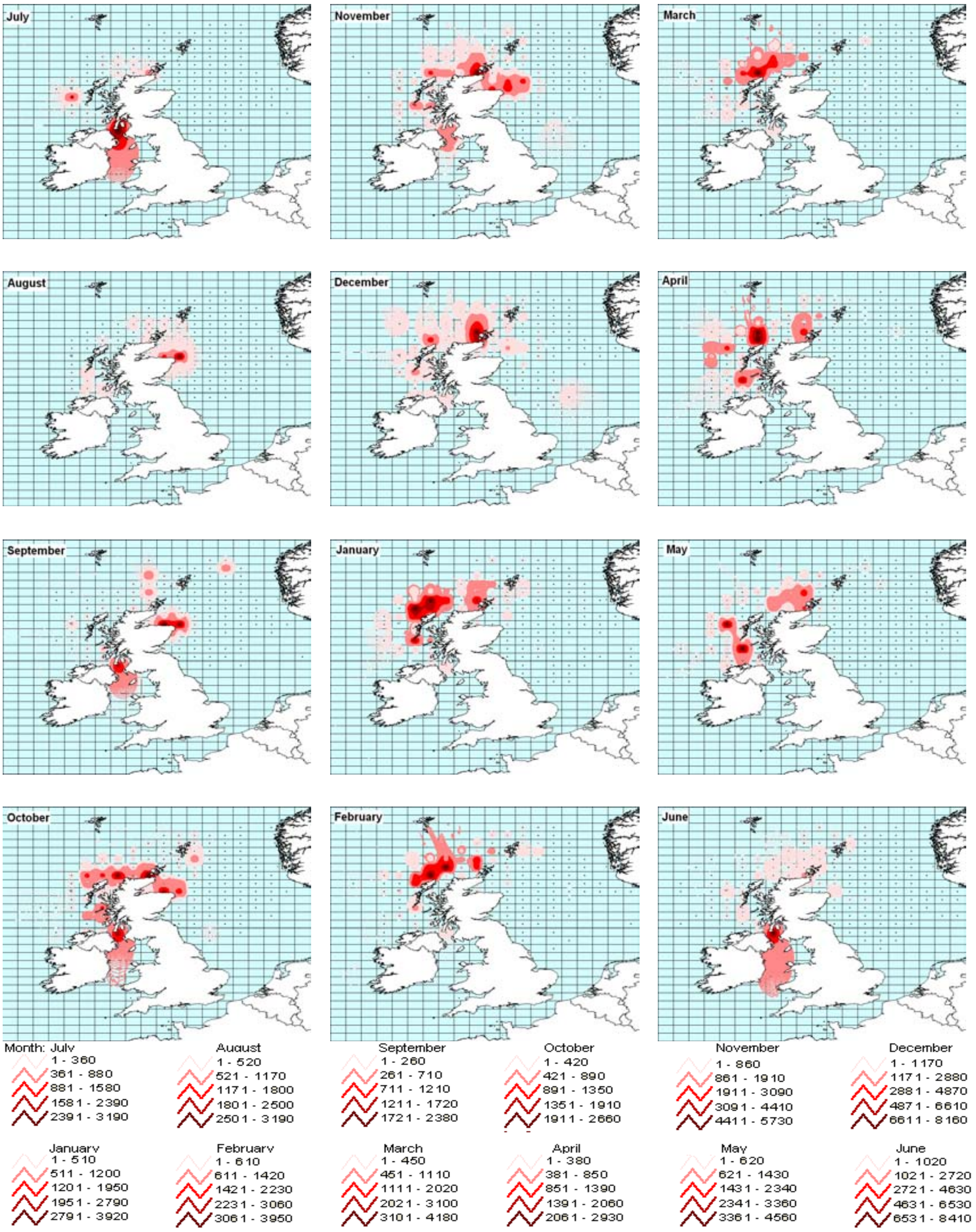


Fig. 14 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1994 until June of the following year, 1995. Black dots represent the presence of haul(s) in the ICES square.

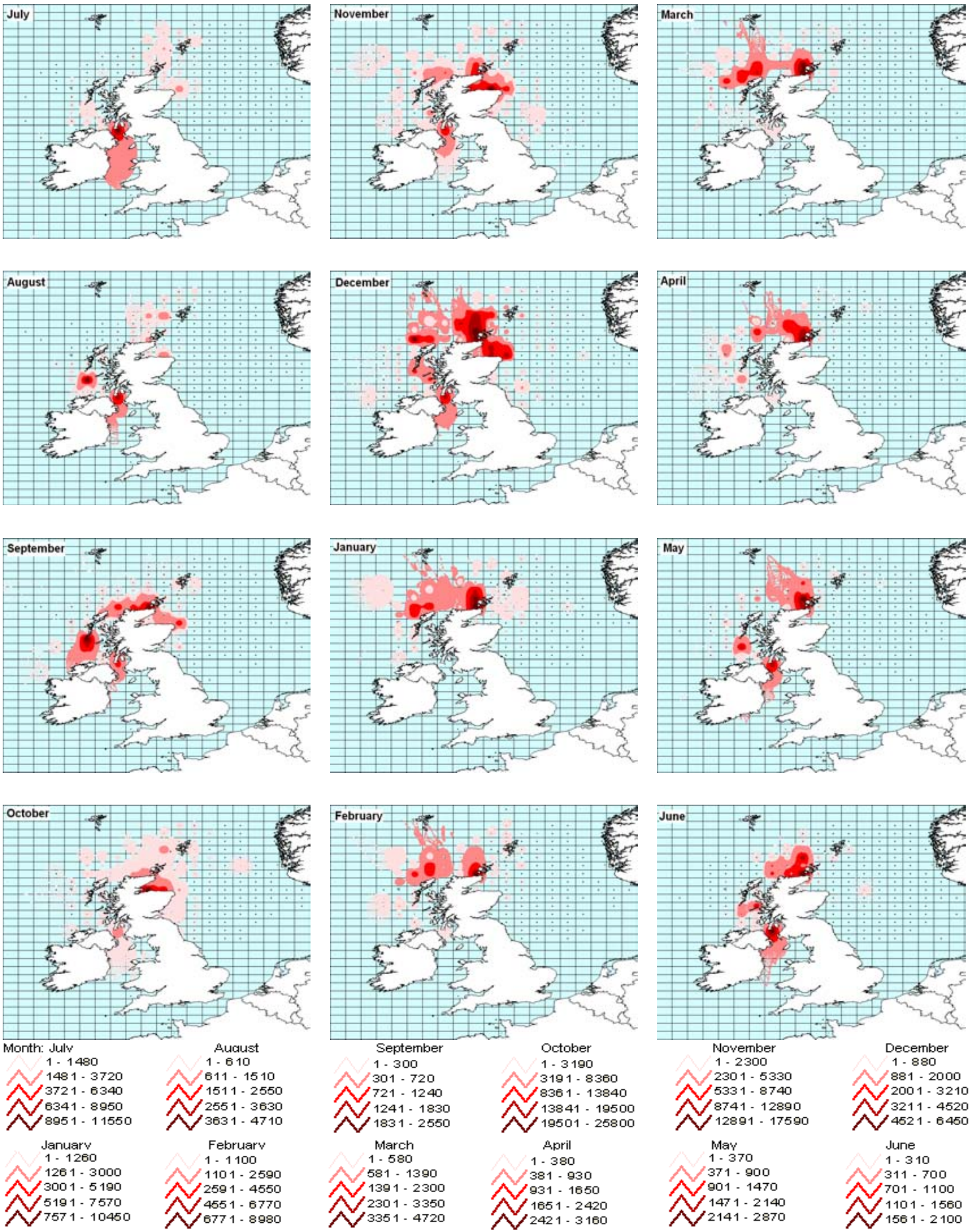


Fig. 15 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1995 until June of the following year, 1996. Black dots represent the presence of haul(s) in the ICES square.

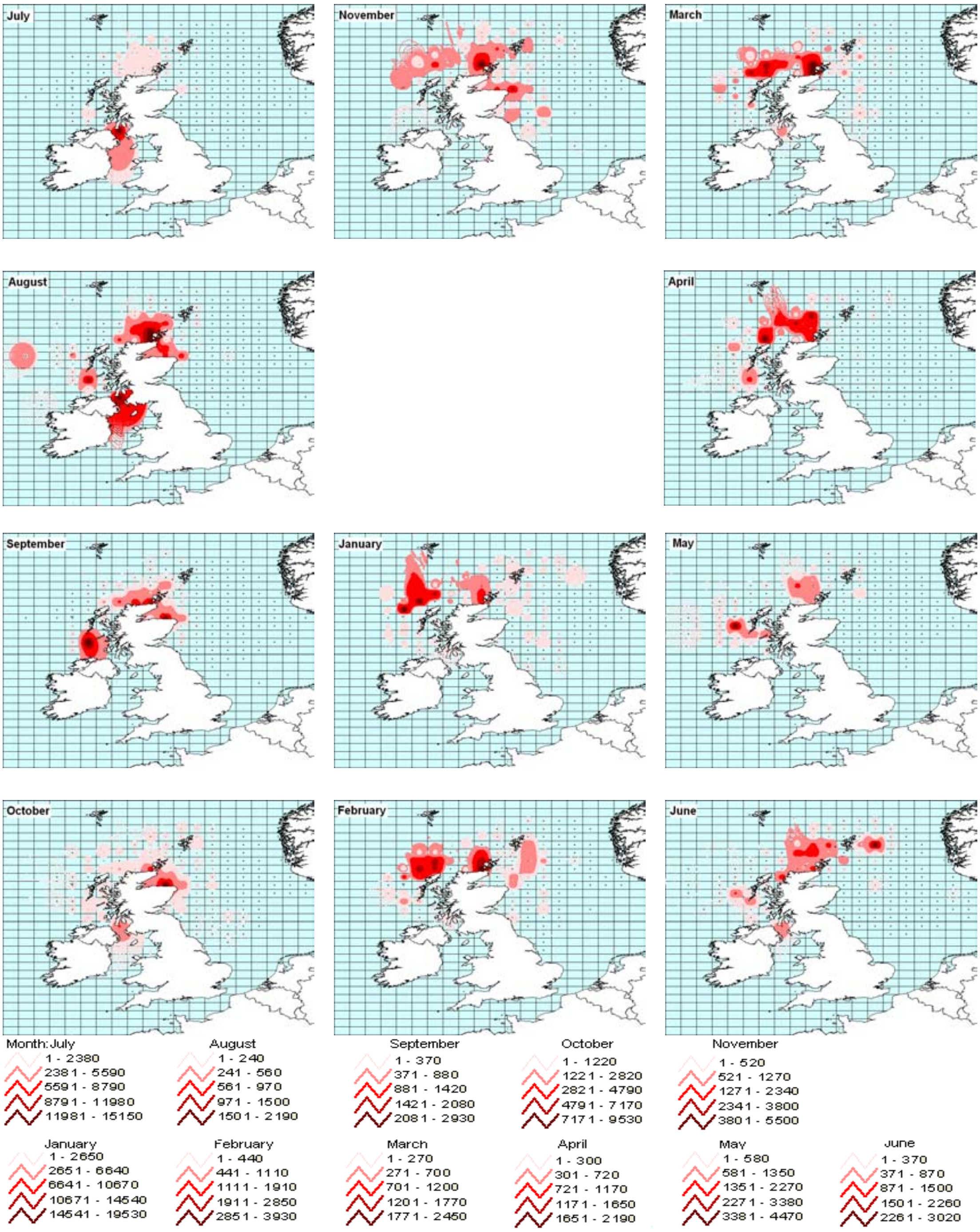


Fig. 16 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1996 until June of the following year, 1997. Black dots represent the presence of haul(s) in the ICES square.

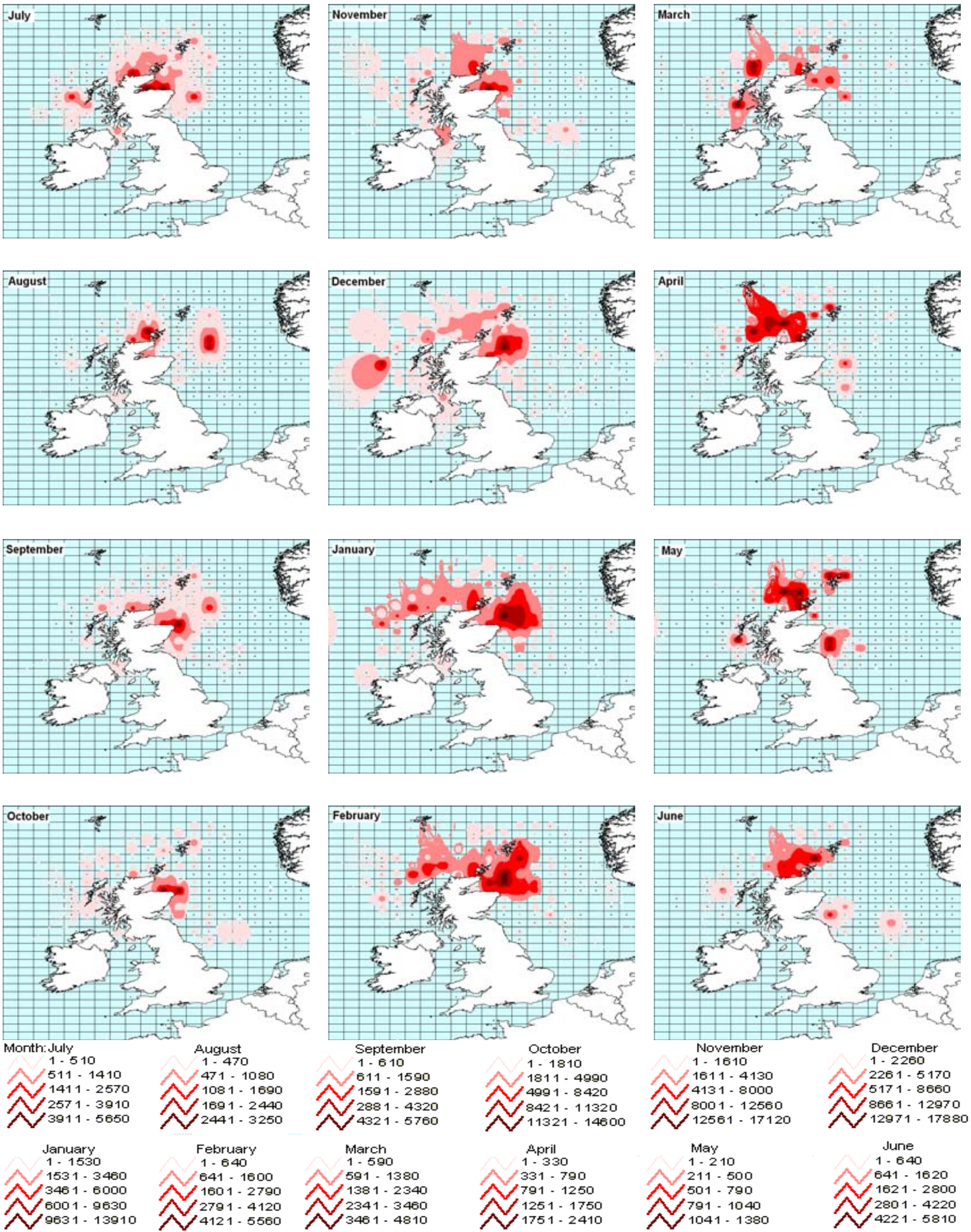


Fig. 17 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1997 until June of the following year, 1998. Black dots represent the presence of haul(s) in the ICES square.

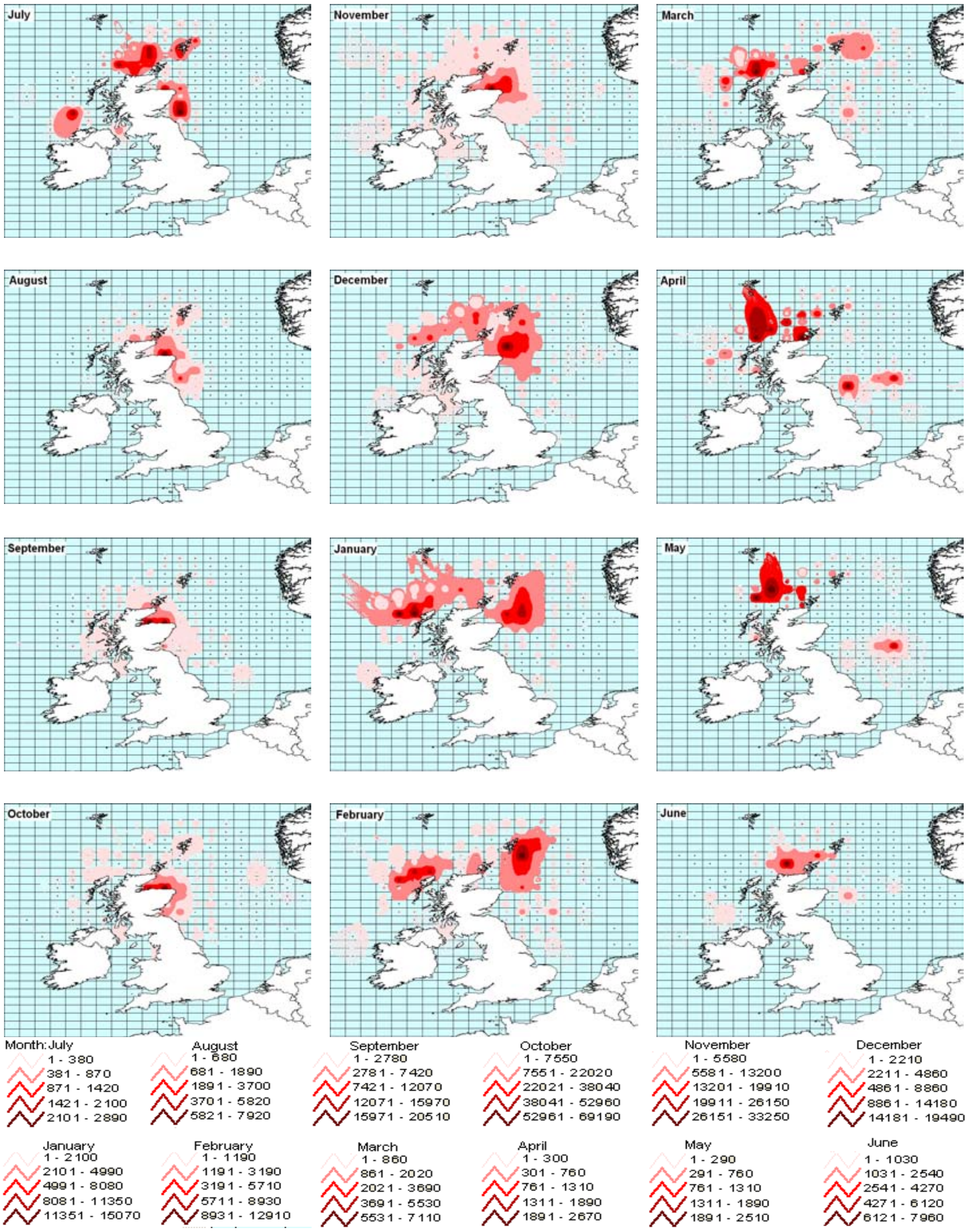


Fig. 18 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1998 until June of the following year, 1999. Black dots represent the presence of haul(s) in the ICES square.

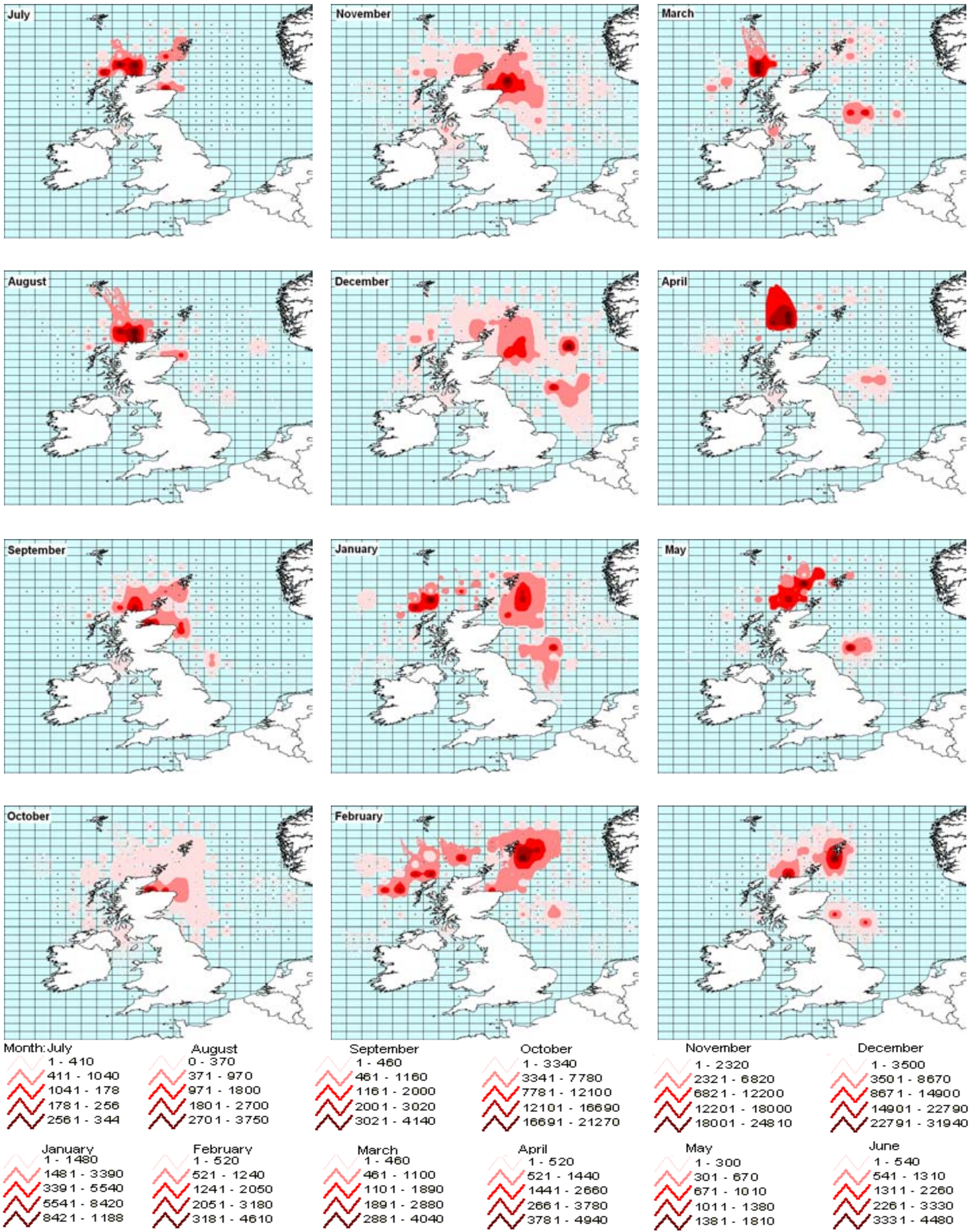


Fig. 19 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 1999 until June of the following year, 2000. Black dots represent the presence of haul(s) in the ICES square.

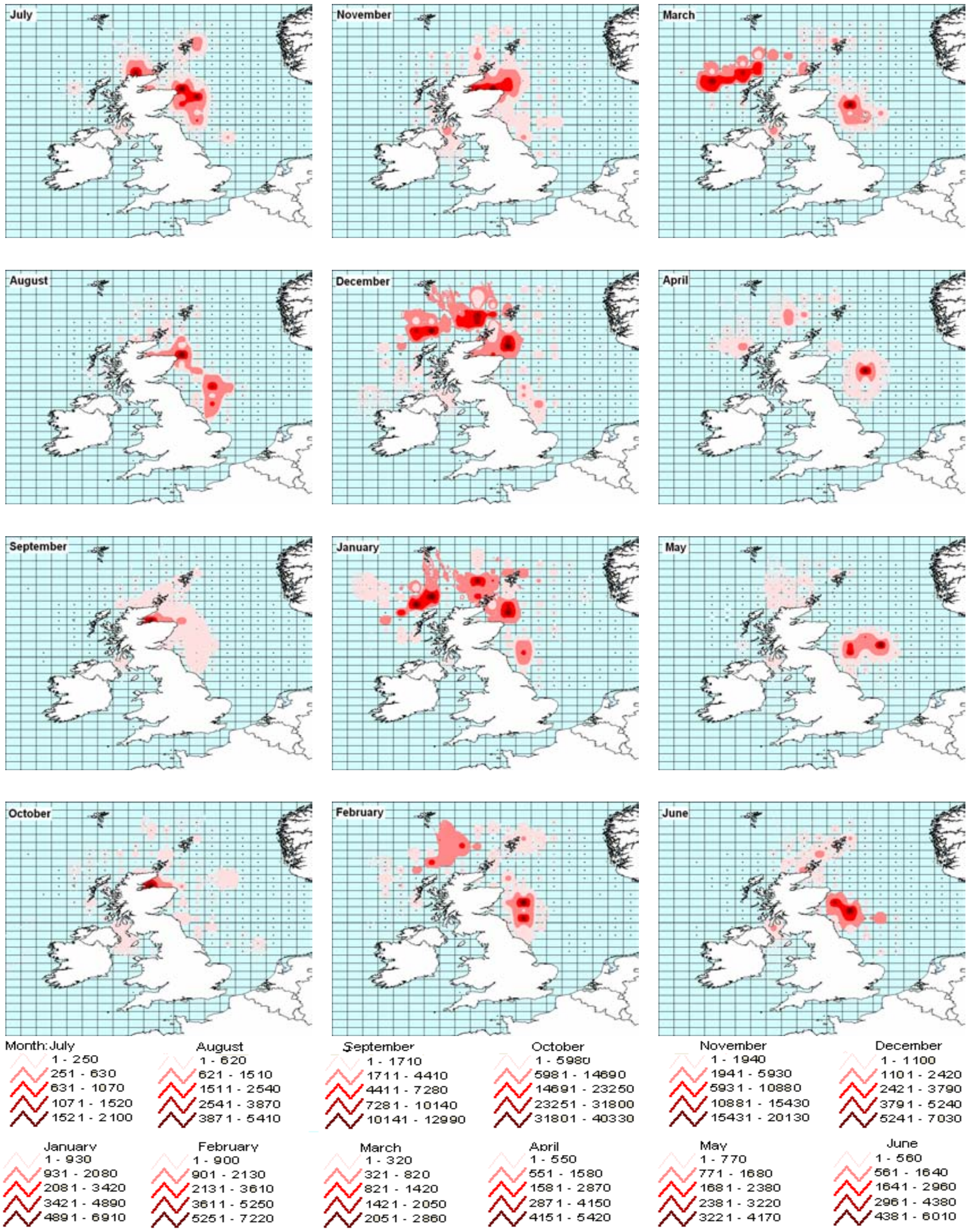


Fig. 20 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 2001 until June of the following year, 2002. Black dots represent the presence of haul(s) in the ICES square.

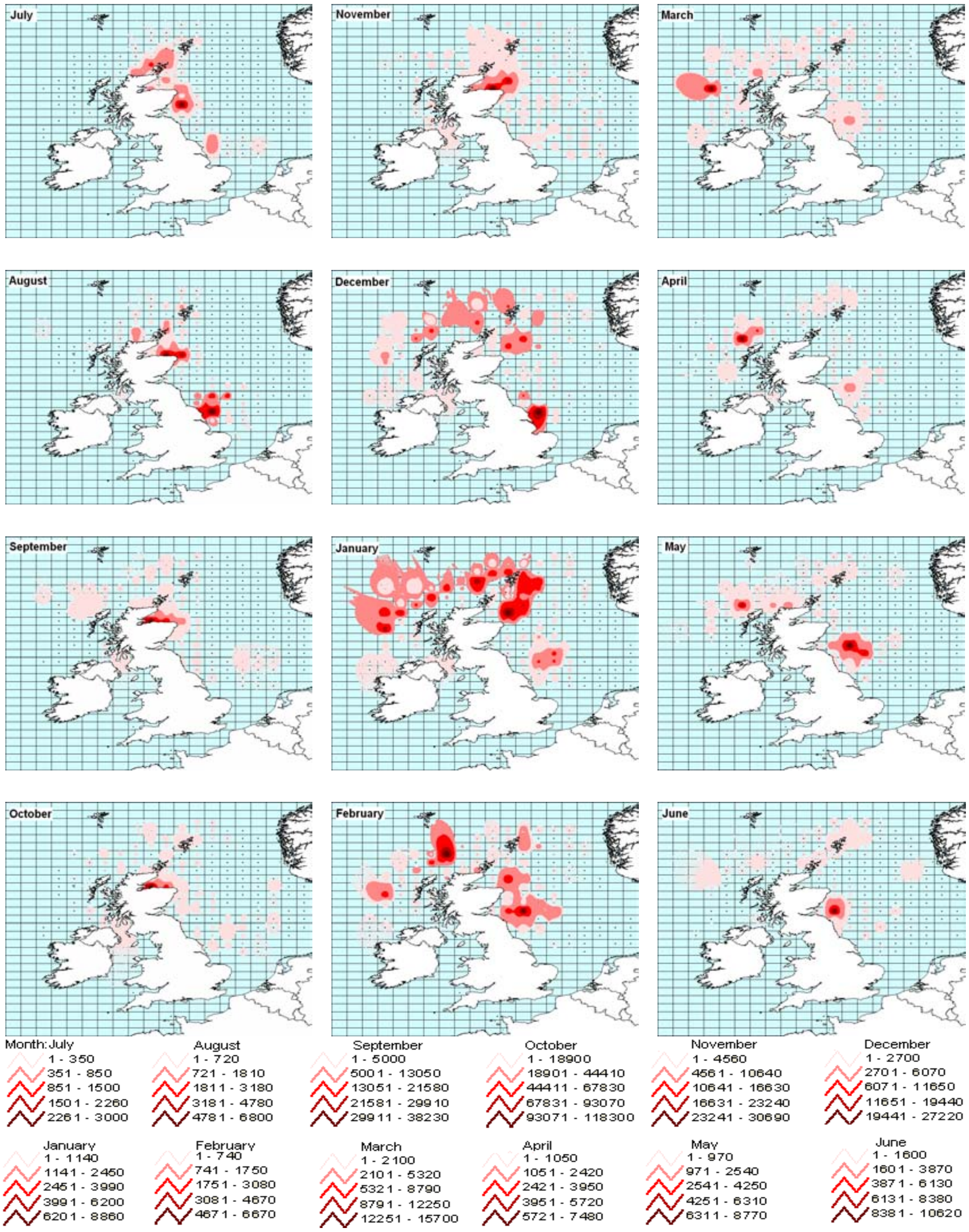


Fig. 21 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 2002 until June of the following year, 2003. Black dots represent the presence of haul(s) in the ICES square.

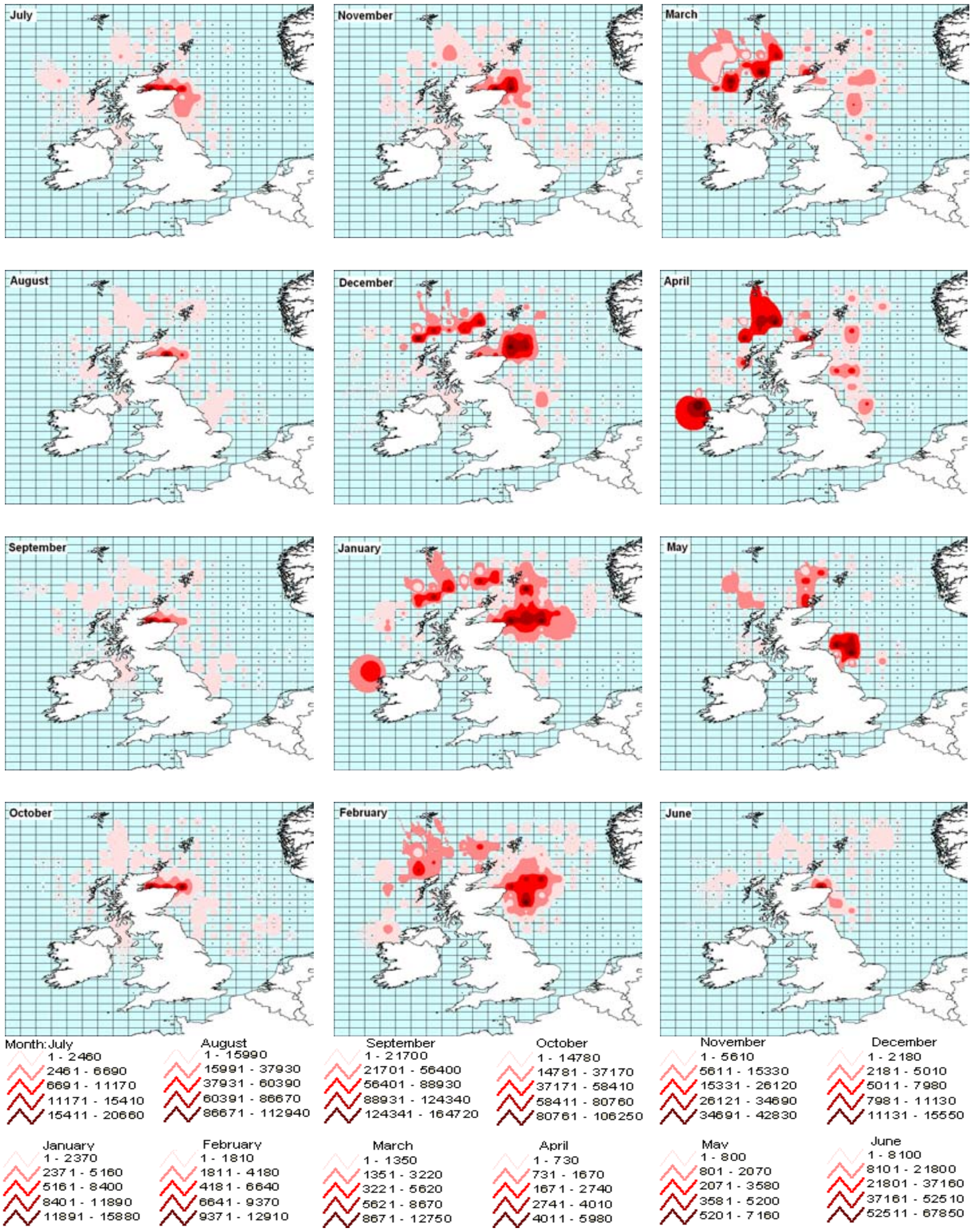


Fig. 22 - Contour maps of the annual distribution of *L. forbesi* abundance, from July of the year 2003 until June of the following year, 2004. Black dots represent the presence of haul(s) in the ICES square.

Appendix IV – Length-frequency analysis graphics

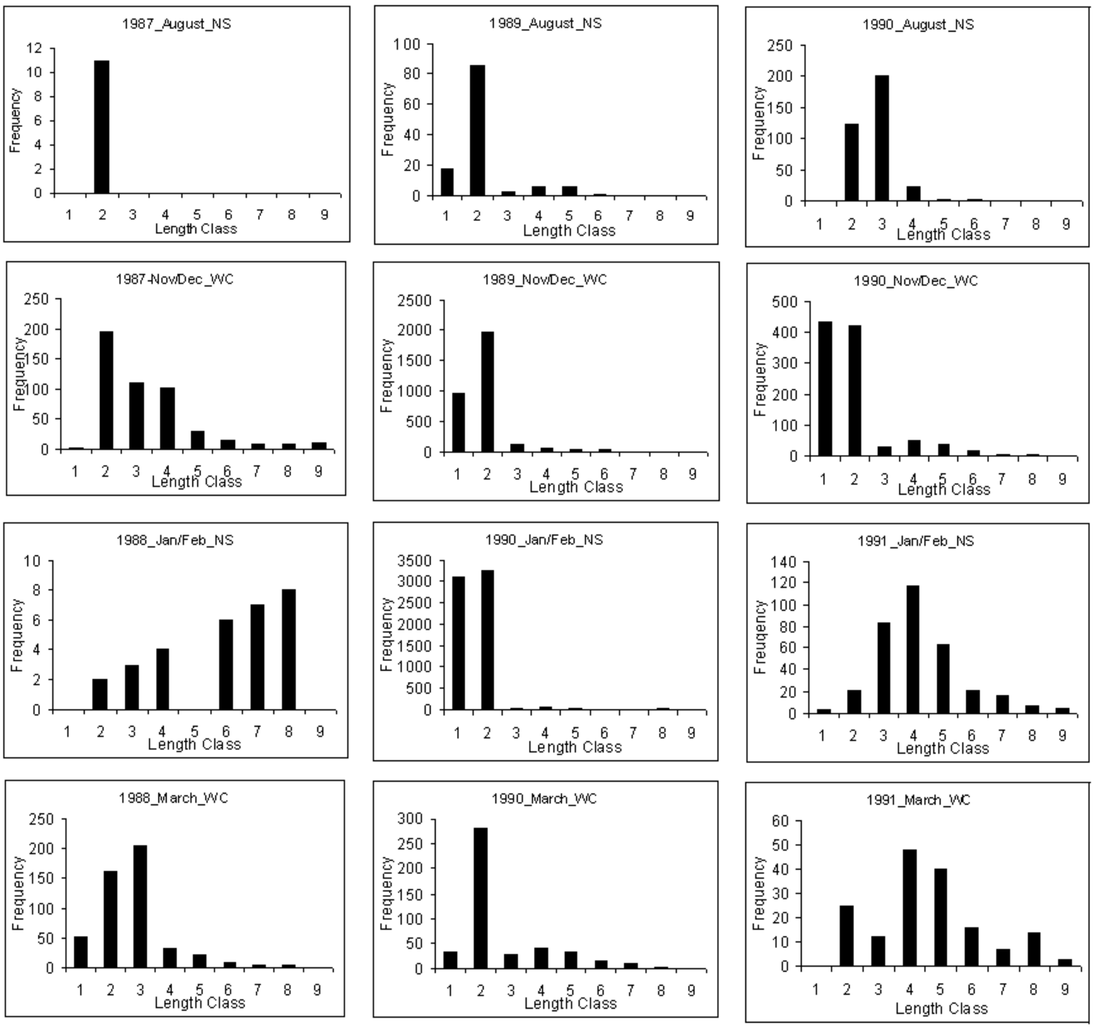


Fig. 1 – *L. forbesi* length-frequency distributions from 1987/1988 (left), 1989/1990 (middle) and 1990/1991 (right). The series starts in August with data from the North Sea (NS) and November-December from the West Coast (WC), and continues to the following year in January-February with data from NS and March from WC. The x-axis represents length class and the y-axis the frequency of squid occurrence (number). Animals of length class 1: 1-4.5cm; length class 2: 5-9.5cm; length class 3: 10-14cm; length class 4: 15-19cm; length class 5: 20-24.5cm; length class 6: 25-29cm; length class 7: 30-34cm; length class 8: 35-44cm; length class 9: 45-73cm.

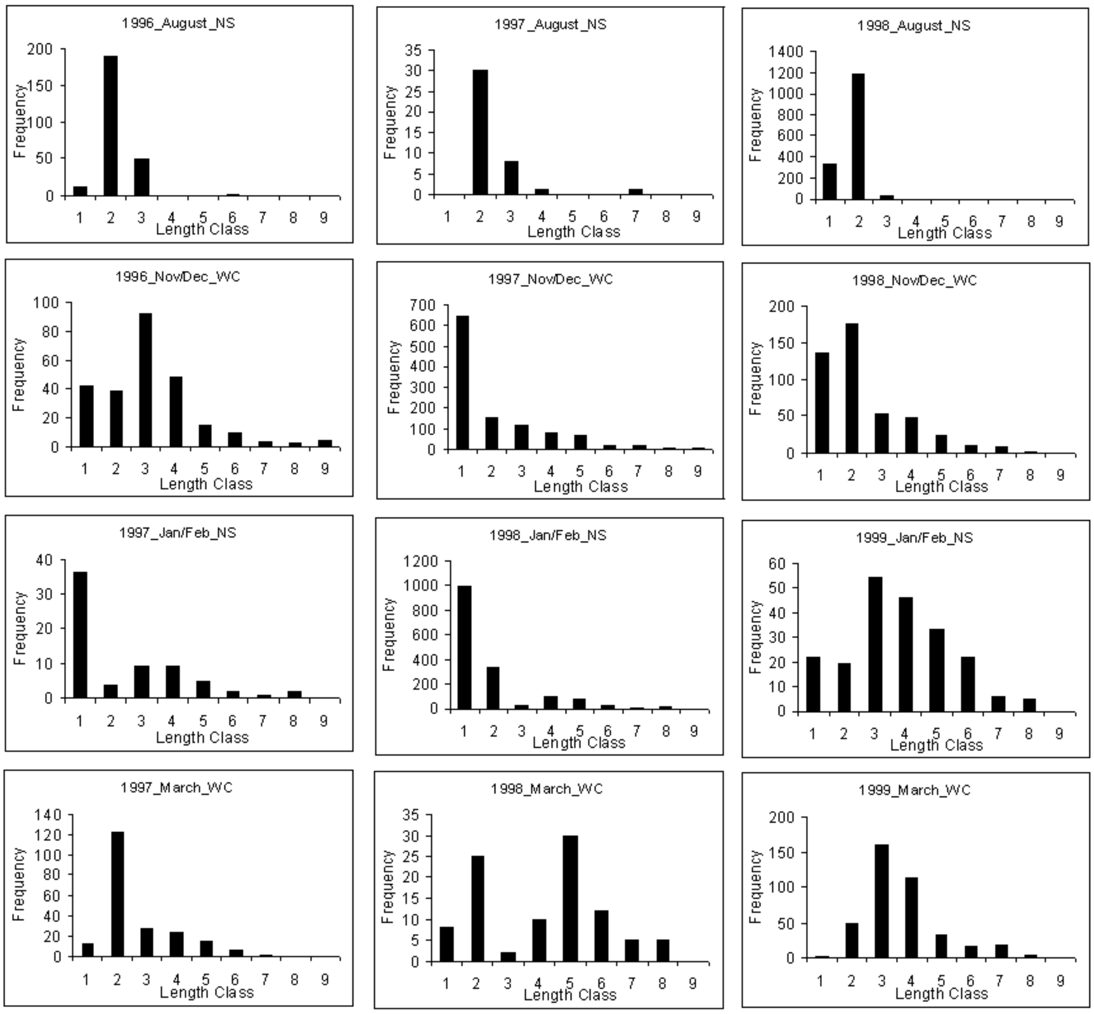


Fig. 2 – *L. forbesi* length-frequency distributions from 1996/1997 (left), 1997/1998 (middle) and 1998/1999 (right). The series starts in August with data from the North Sea (NS) and November-December from the West Coast (WC), and continues to the following year in January-February with data from NS and March from WC. The x-axis represents length class and the y-axis the frequency of squid occurrence (number). Animals of length class 1: 1-4.5cm; length class 2: 5-9.5cm; length class 3: 10-14cm; length class 4: 15-19cm; length class 5: 20-24.5cm; length class 6: 25-29cm; length class 7: 30-34cm; length class 8: 35-44cm; length class 9: 45-73cm.

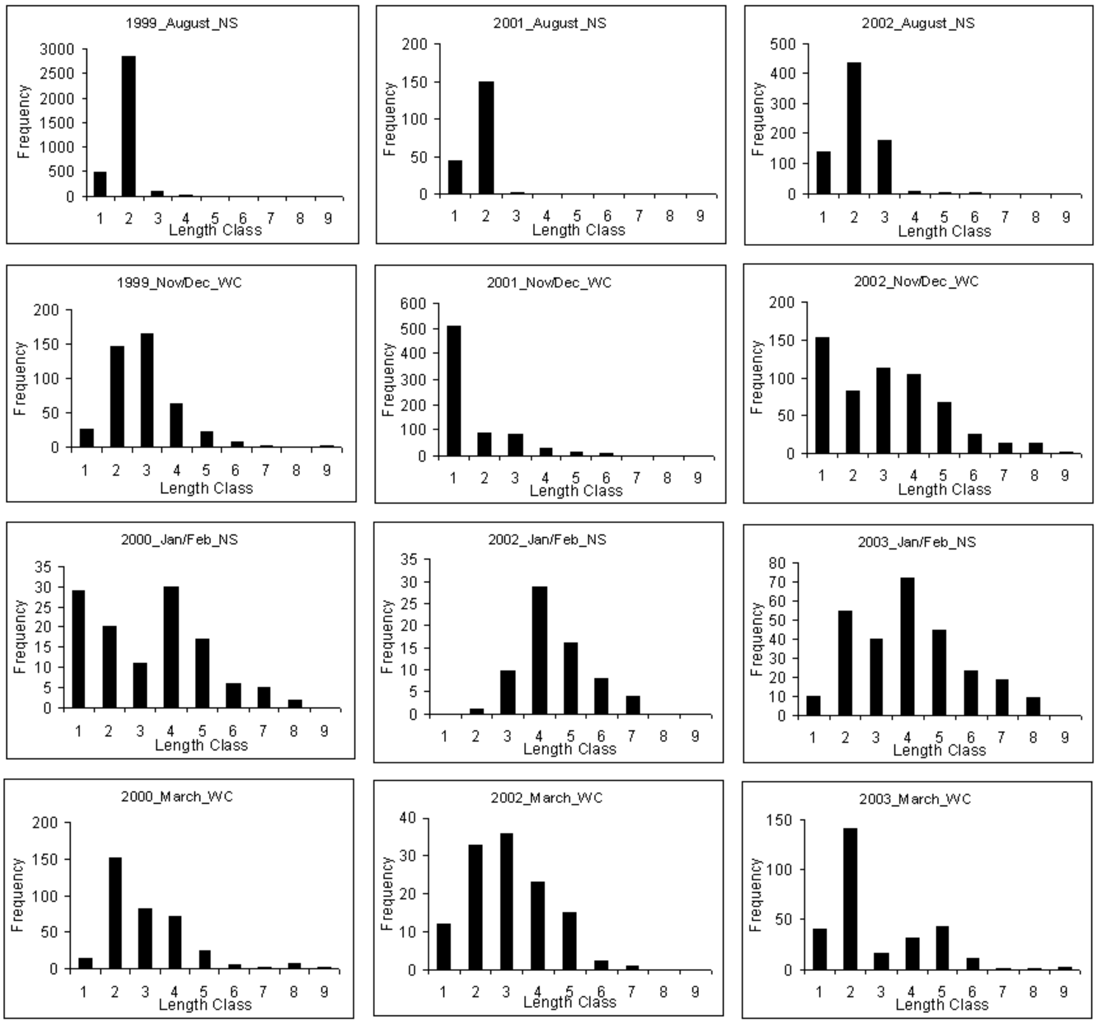


Fig. 3 – *L. forbesi* length-frequency distributions from 1999/2000 (left), 2001/2002 (middle) and 2002/2003 (right). The series starts in August with data from the North Sea (NS) and November-December from the West Coast (WC), and continues to the following year in January-February with data from NS and March from WC. The x-axis represents length class and the y-axis the frequency of squid occurrence (number). Animals of length class 1: 1-4.5cm; length class 2: 5-9.5cm; length class 3: 10-14cm; length class 4: 15-19cm; length class 5: 20-24.5cm; length class 6: 25-29cm; length class 7: 30-34cm; length class 8: 35-44cm; length class 9: 45-73cm.

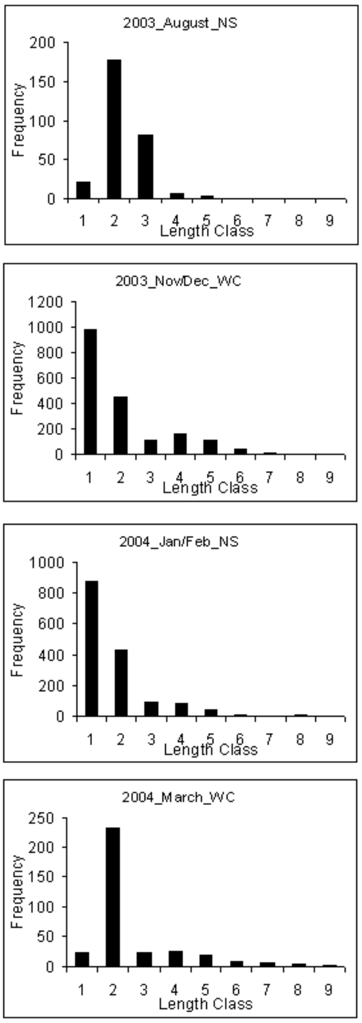


Fig. 4 – *L. forbesi* length-frequency distributions from 2003/2004. The series starts in August with data from the North Sea (NS) and November-December from the West Coast (WC), and continues to the following year in January-February with data from NS and March from WC. The x-axis represents length class and the y-axis the frequency of squid occurrence (number). Animals of length class 1: 1-4.5cm; length class 2: 5-9.5cm; length class 3: 10-14cm; length class 4: 15-19cm; length class 5: 20-24.5cm; length class 6: 25-29cm; length class 7: 30-34cm; length class 8: 35-44cm; length class 9: 45-73cm.

Appendix V – Distance to coast of landings

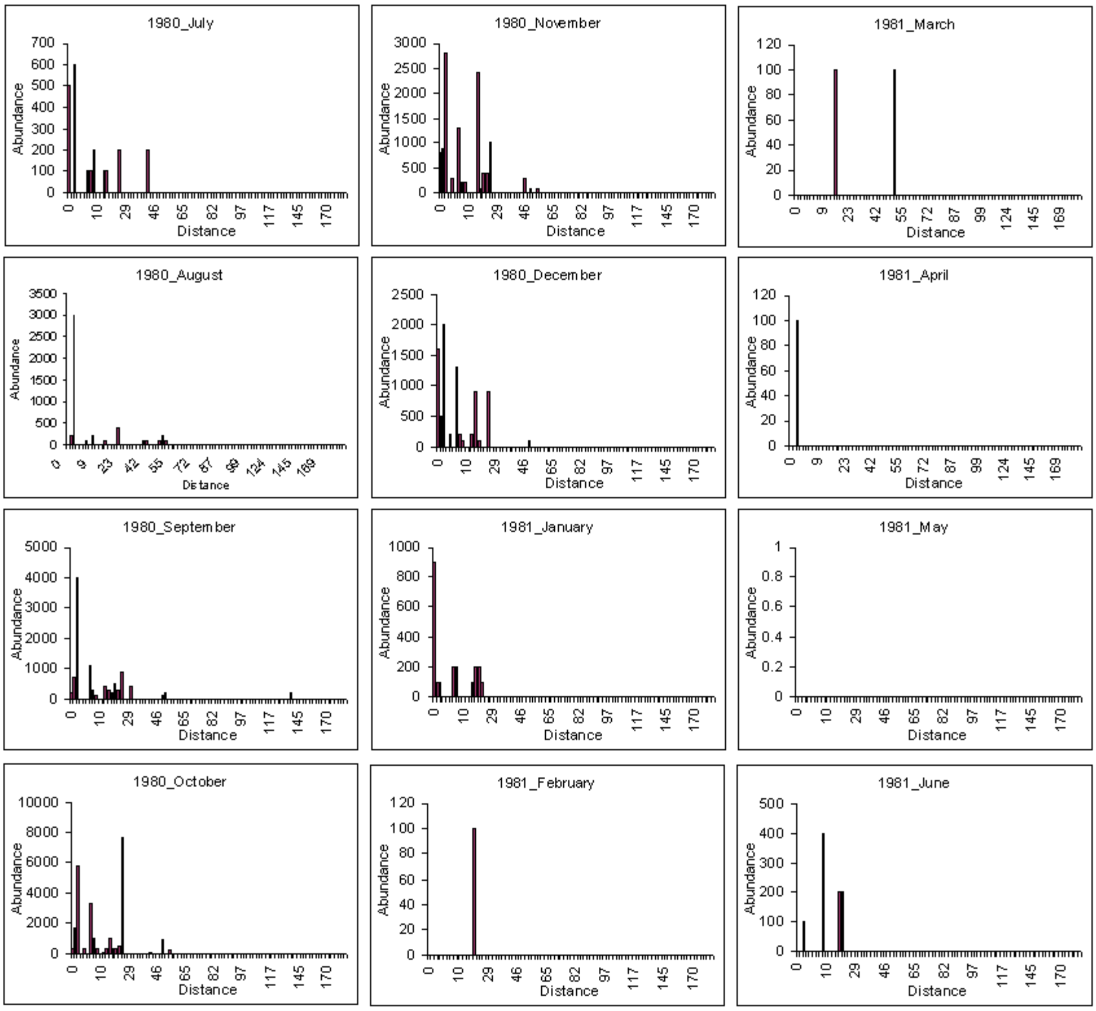


Fig. 1 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1980, starting in July and finishing in June of the following year, 1981.

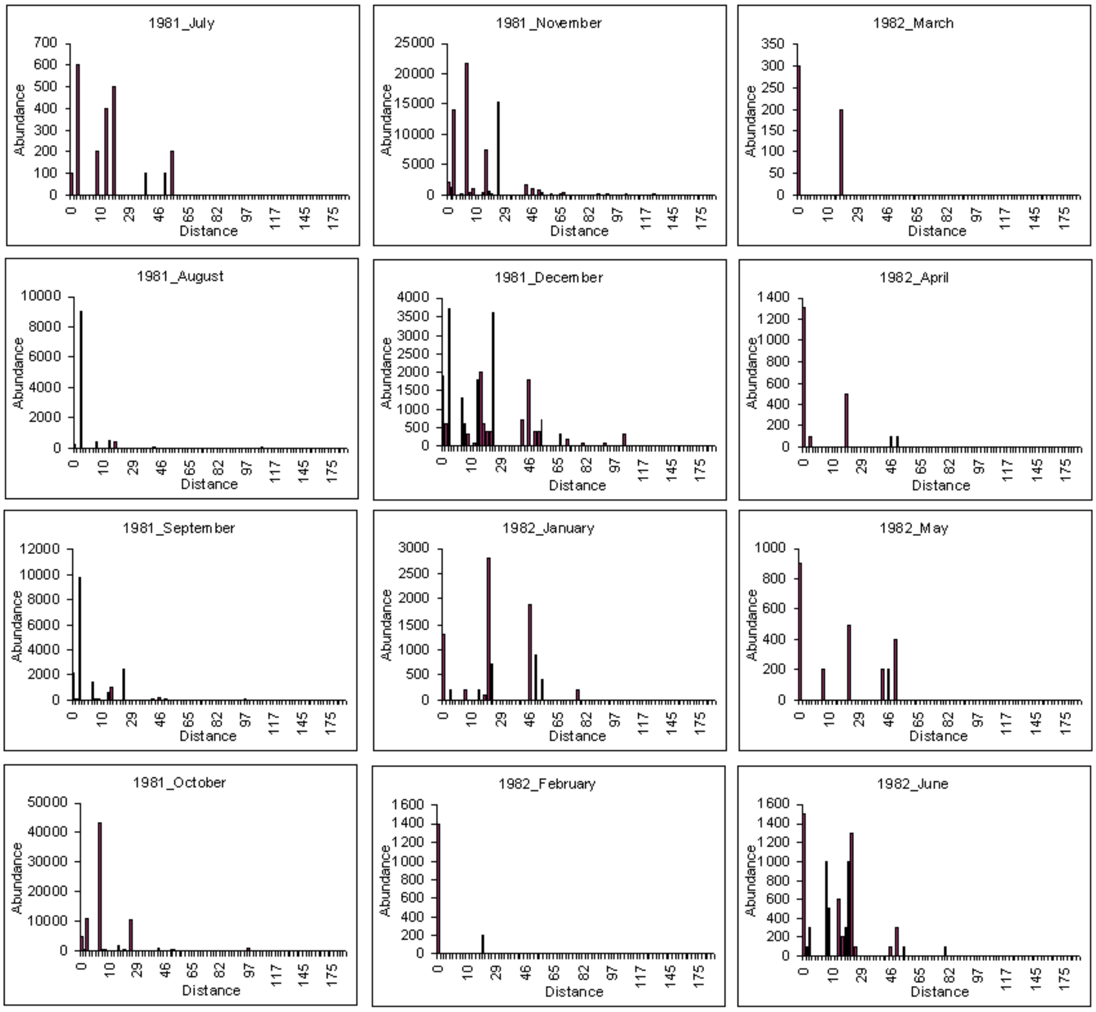


Fig. 2 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1981, starting in July and finishing in June of the following year, 1982.

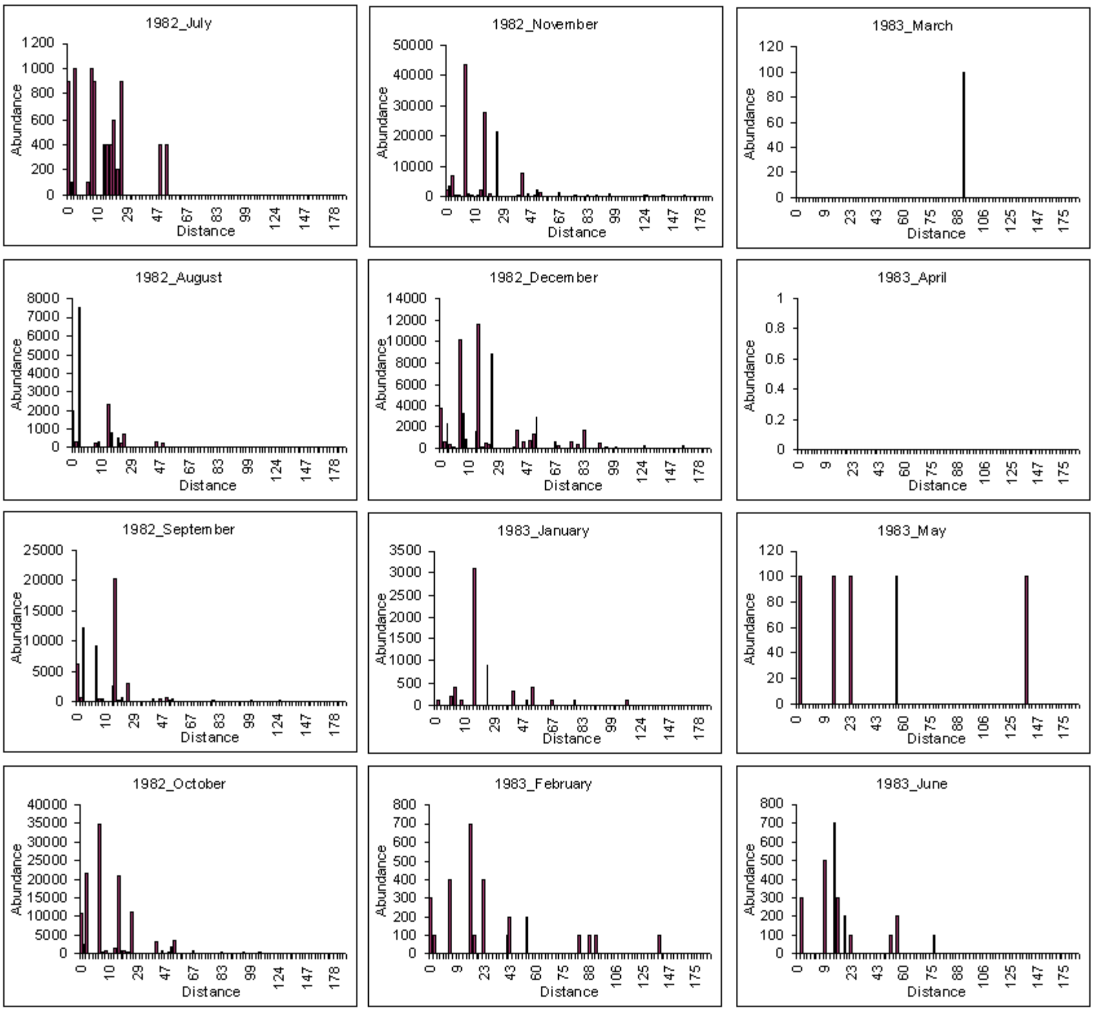


Fig. 3 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1982, starting in July and finishing in June of the following year, 1983.

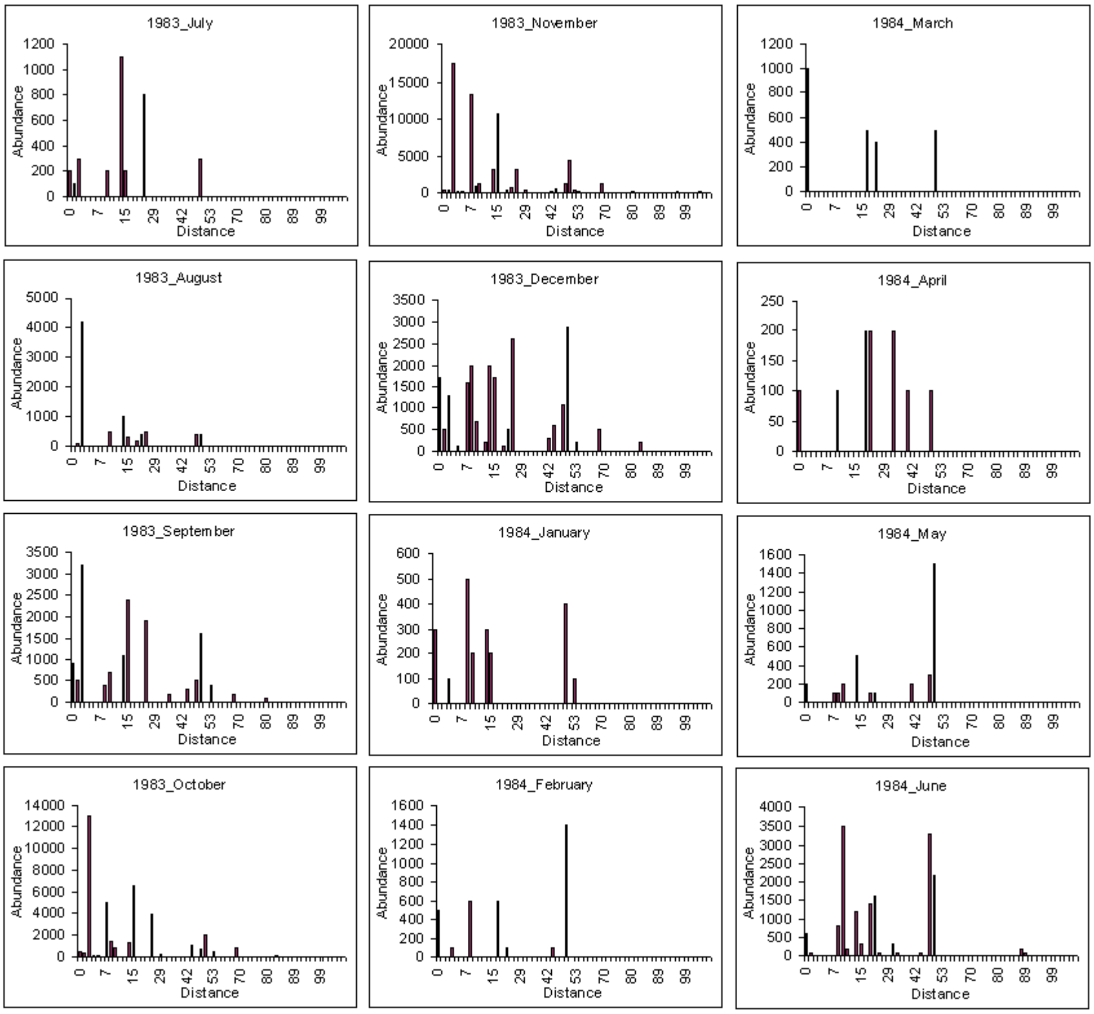


Fig. 4 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1983, starting in July and finishing in June of the following year, 1984.

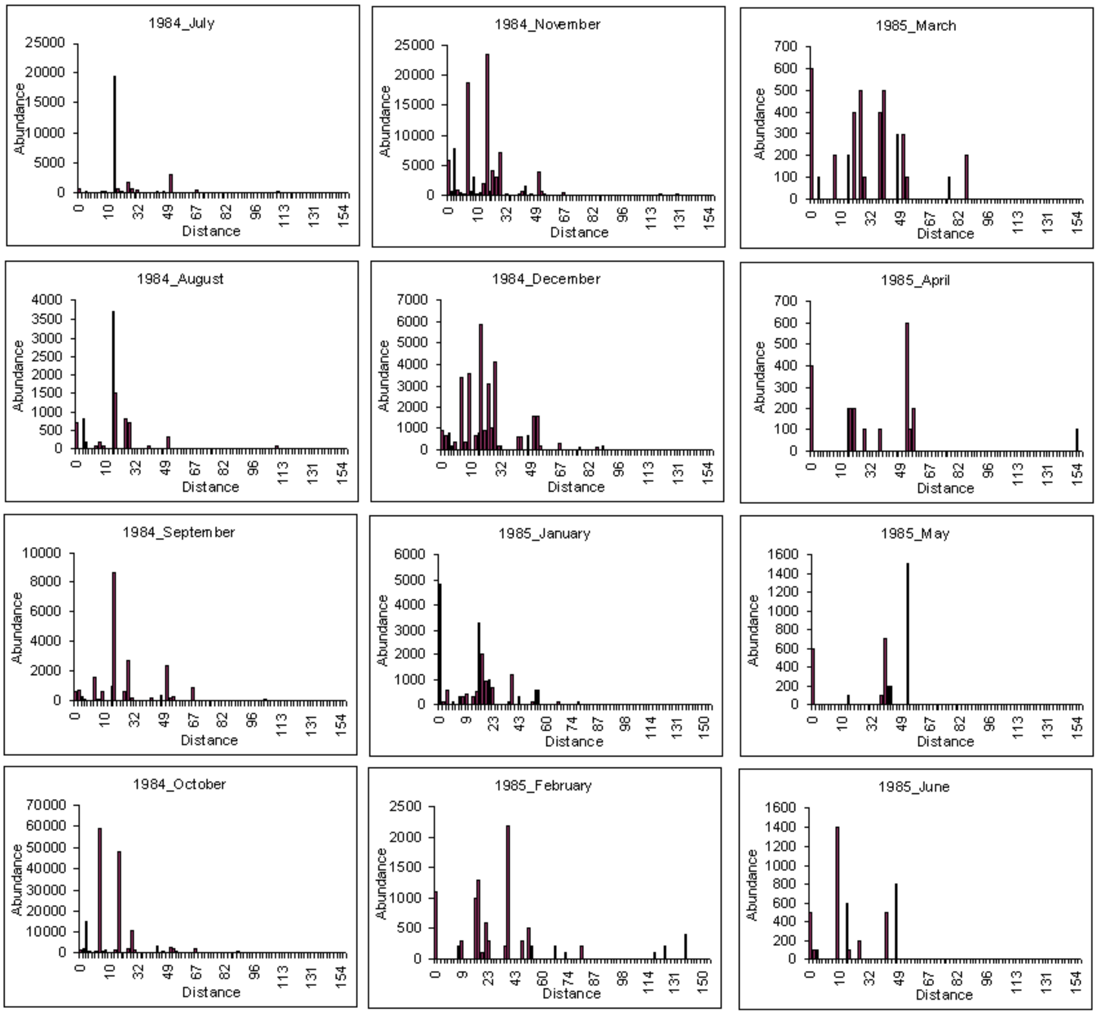


Fig. 5 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1984, starting in July and finishing in June of the following year, 1985.

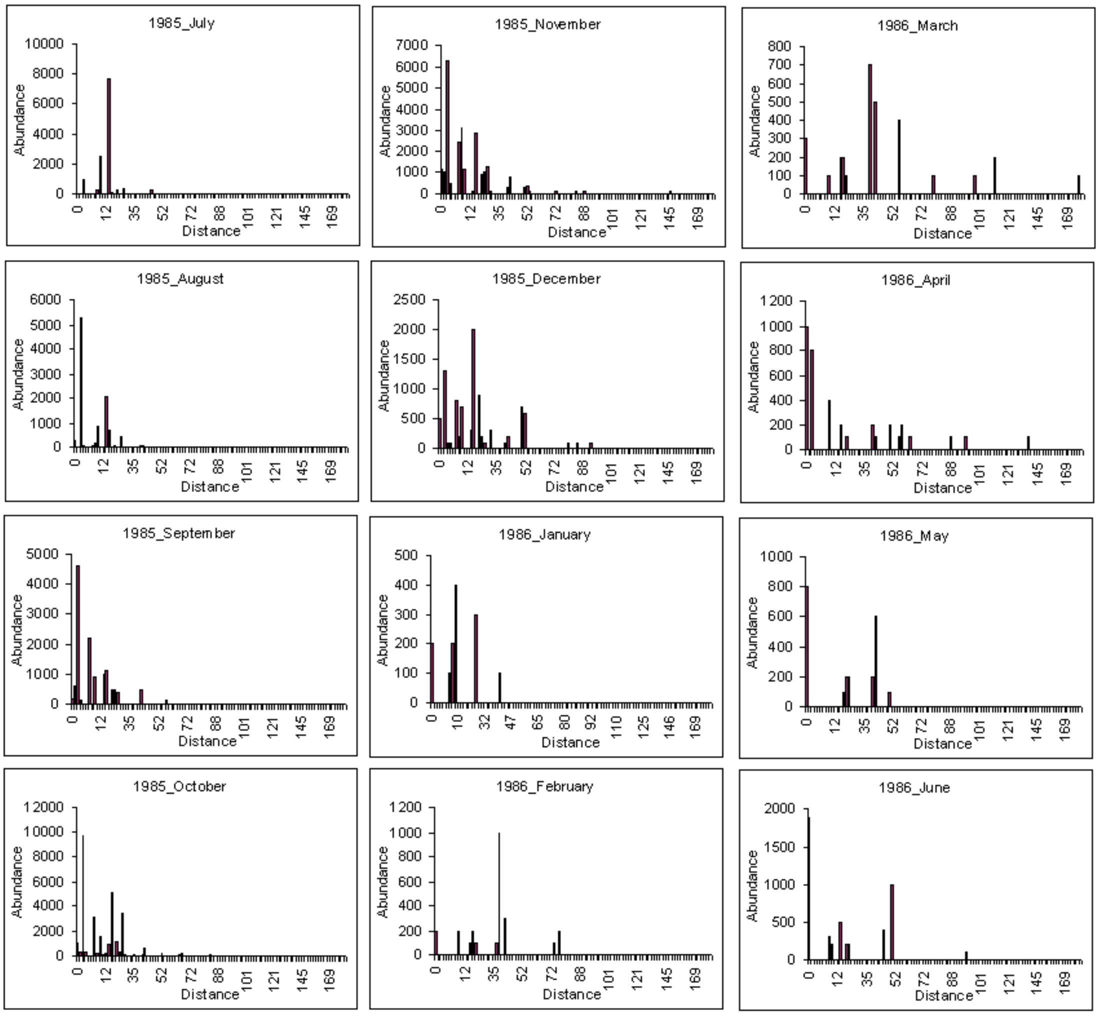


Fig. 6 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1985, starting in July and finishing in June of the following year, 1986.

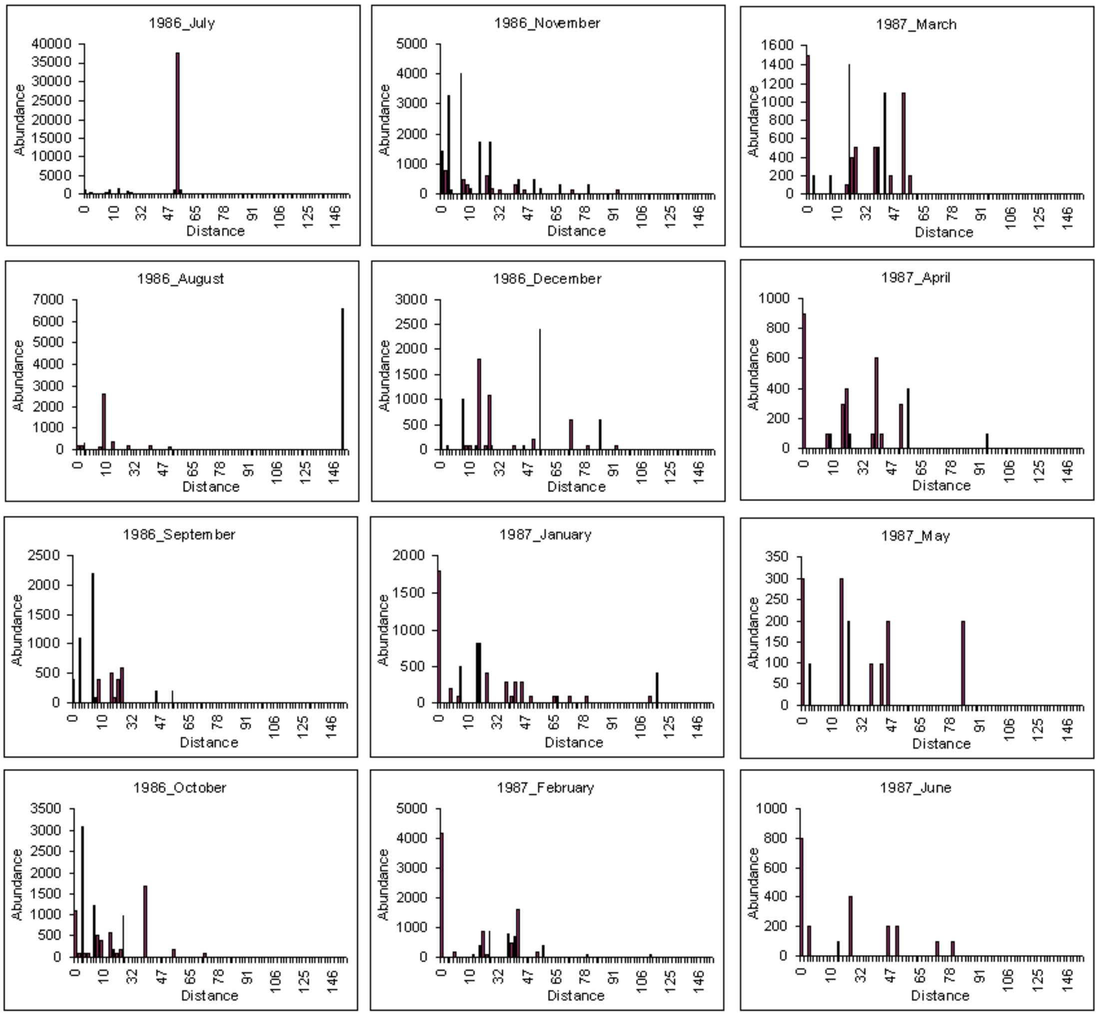


Fig. 7 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1986, starting in July and finishing in June of the following year, 1987.

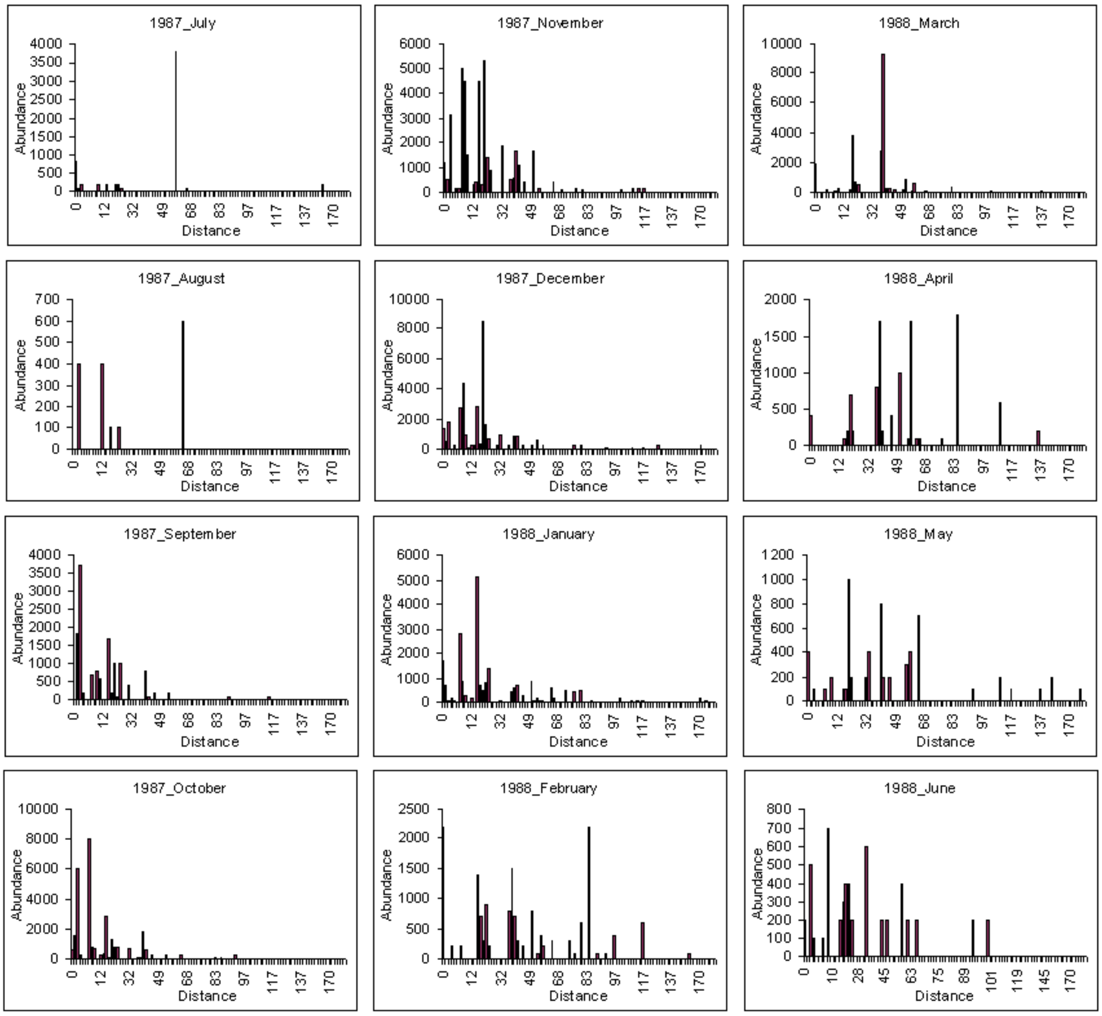


Fig. 8 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1987, starting in July and finishing in June of the following year, 1988.

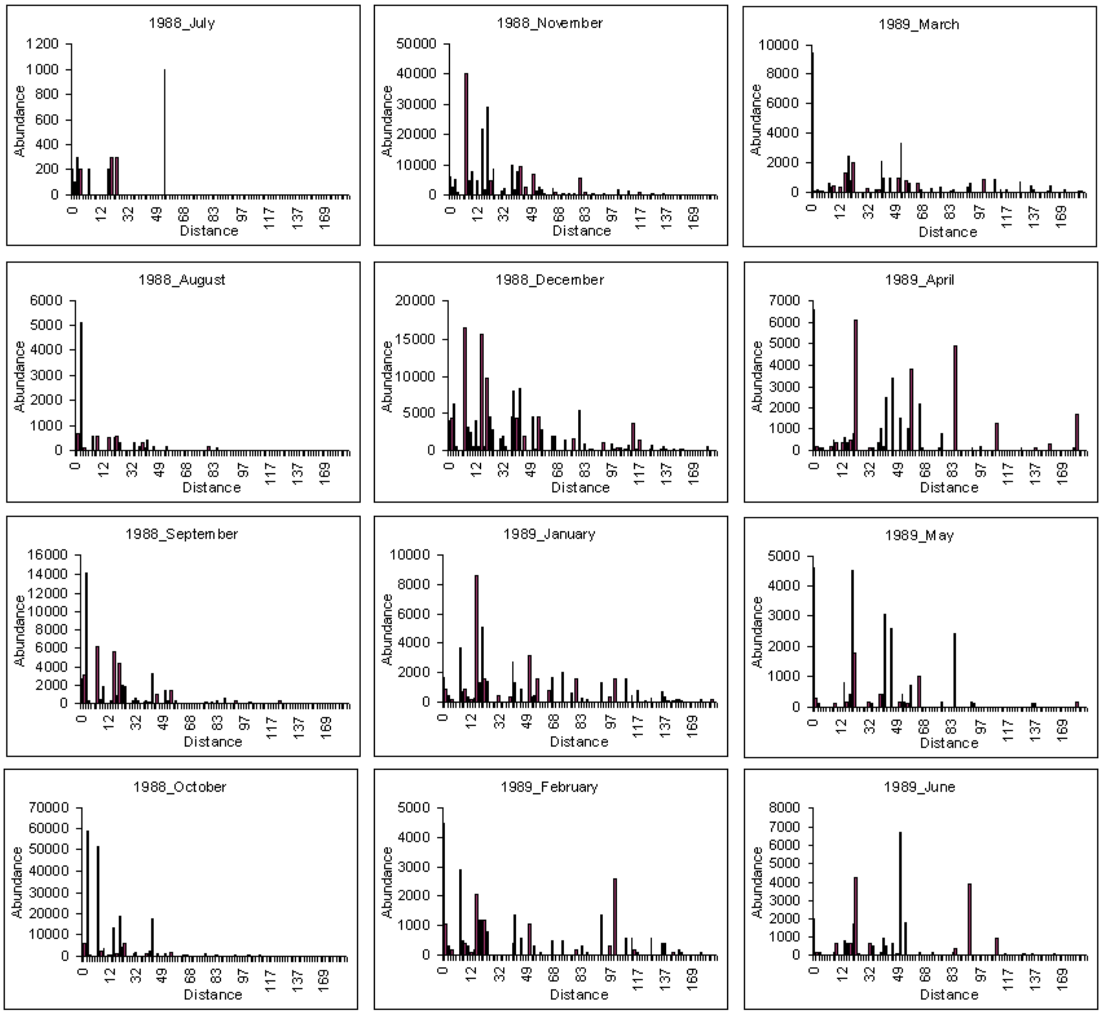


Fig. 9 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1988, starting in July and finishing in June of the following year, 1989.

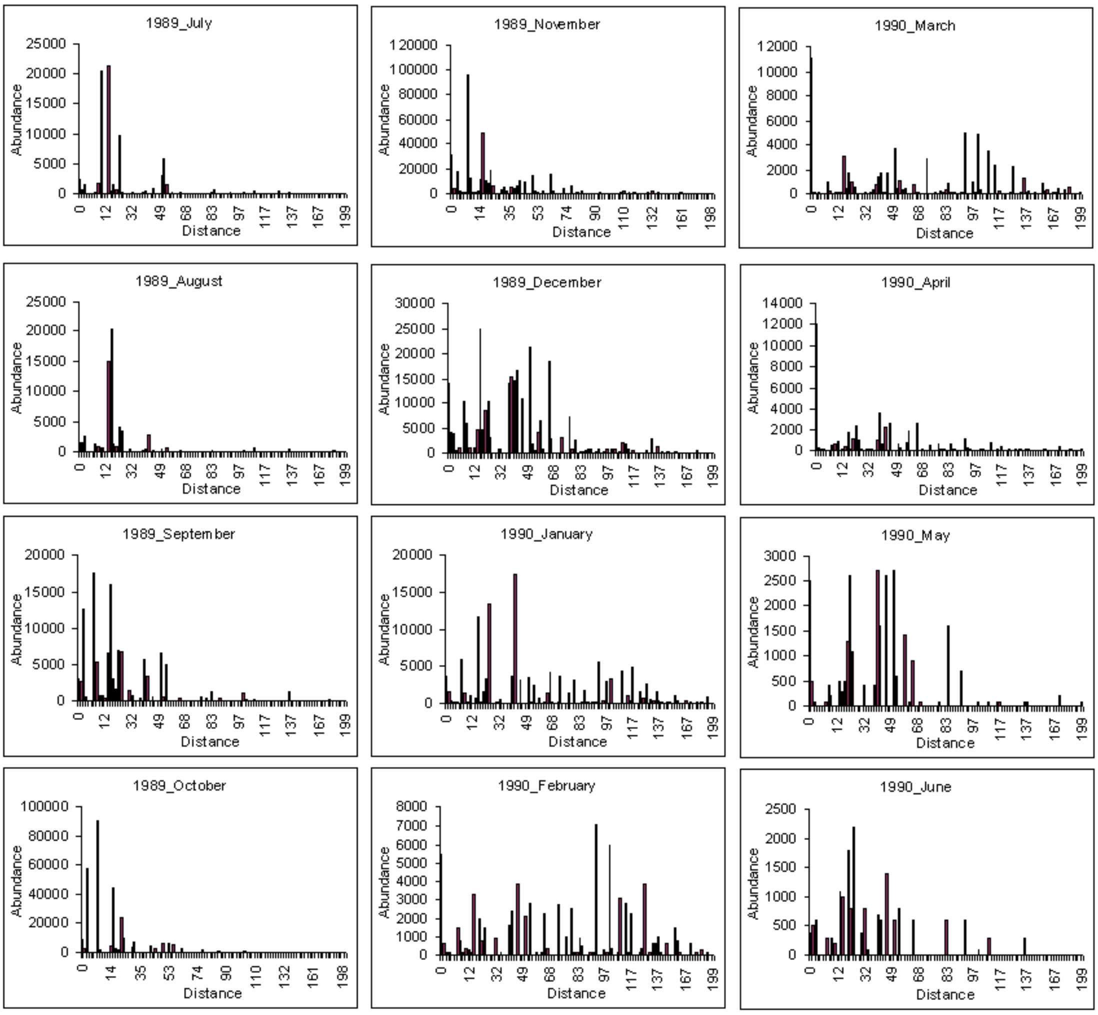


Fig. 10 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1989, starting in July and finishing in June of the following year, 1990.

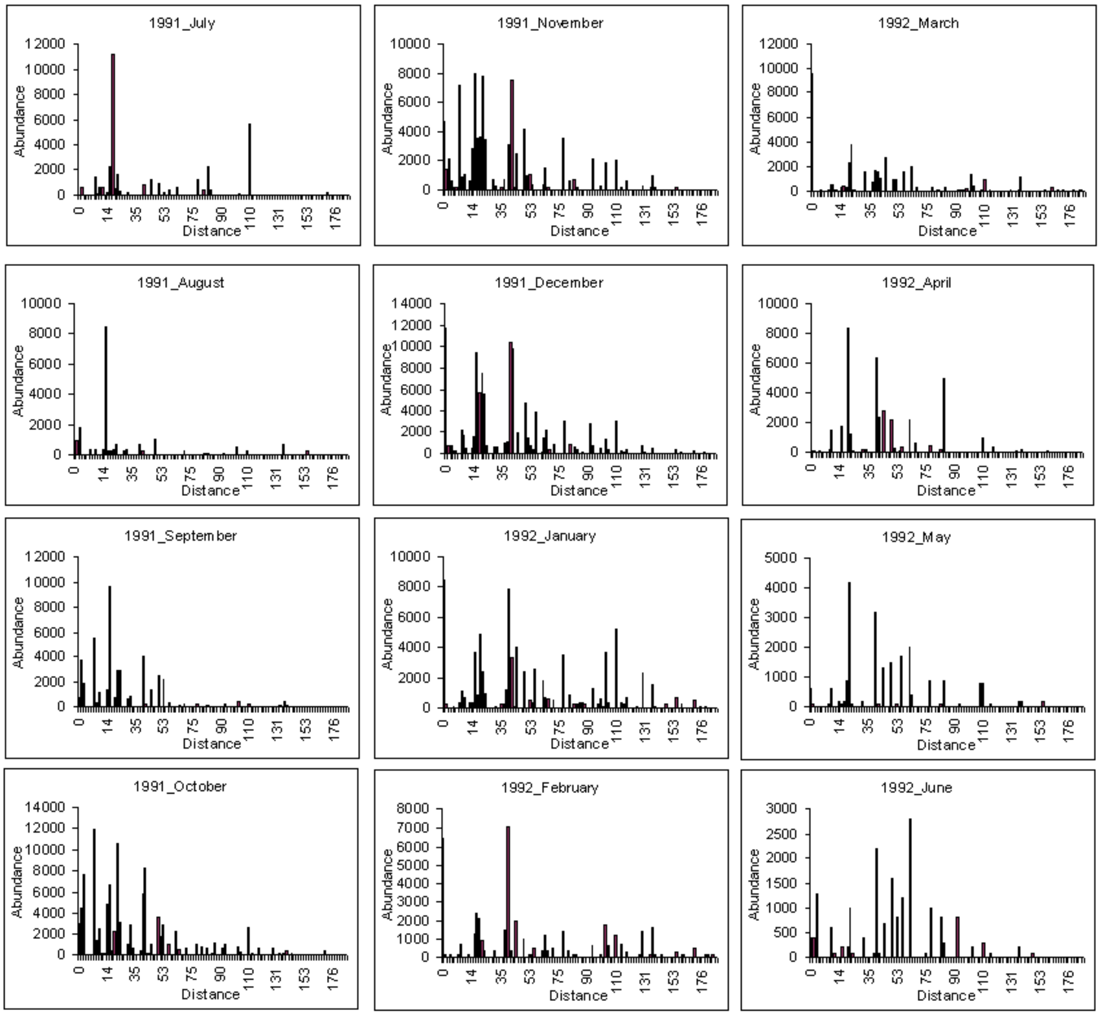


Fig. 11 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1991, starting in July and finishing in June of the following year, 1992.

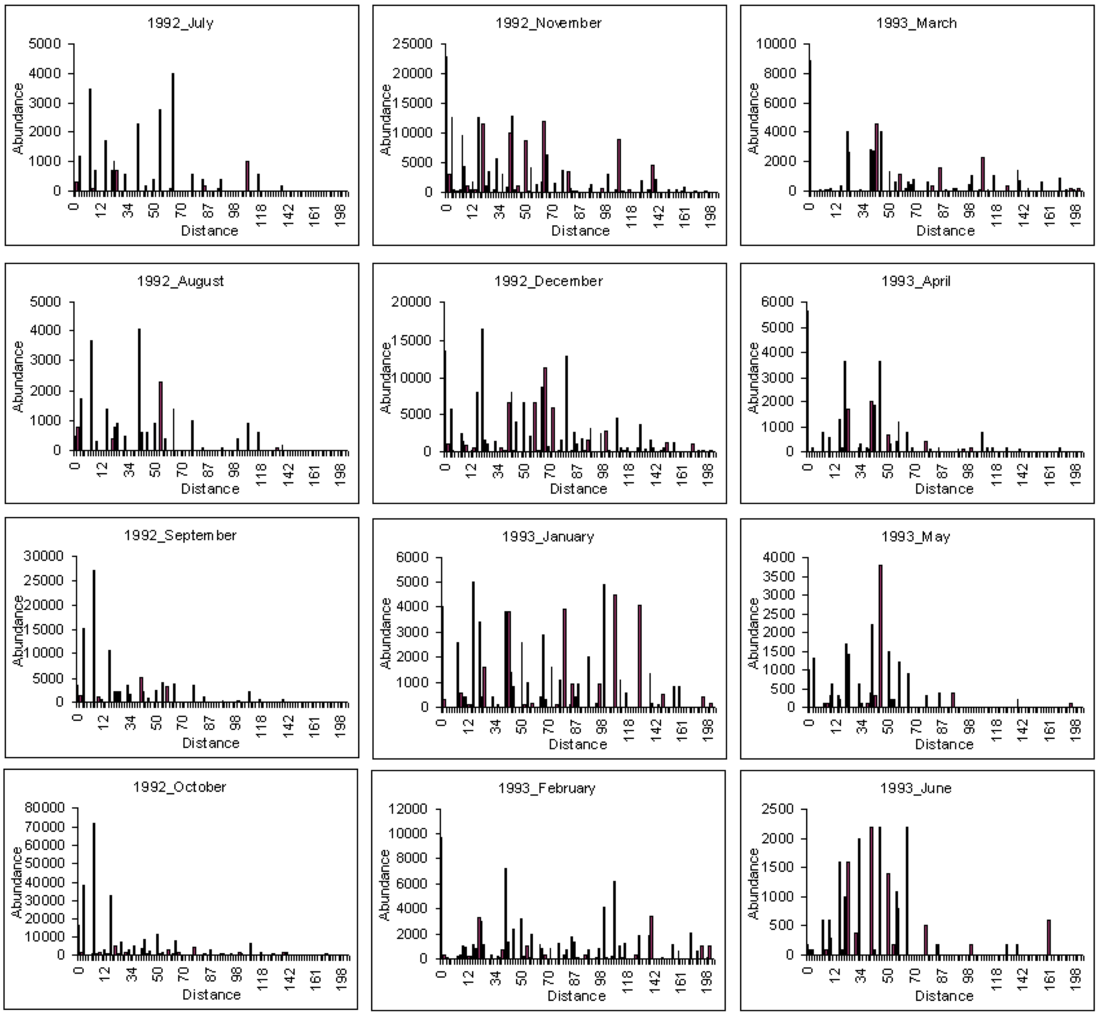


Fig. 12 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1992, starting in July and finishing in June of the following year, 1993.

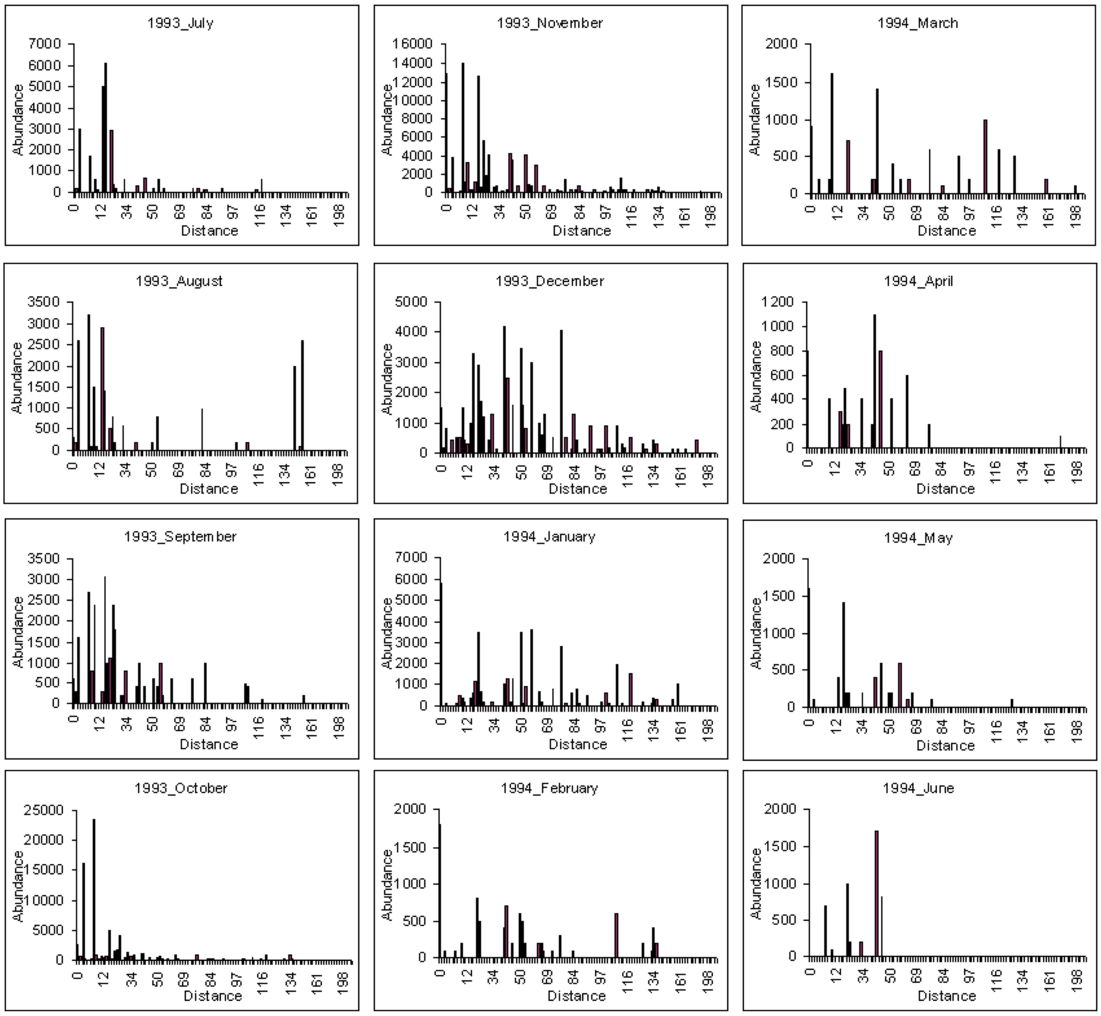


Fig. 13 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1993, starting in July and finishing in June of the following year, 1994.

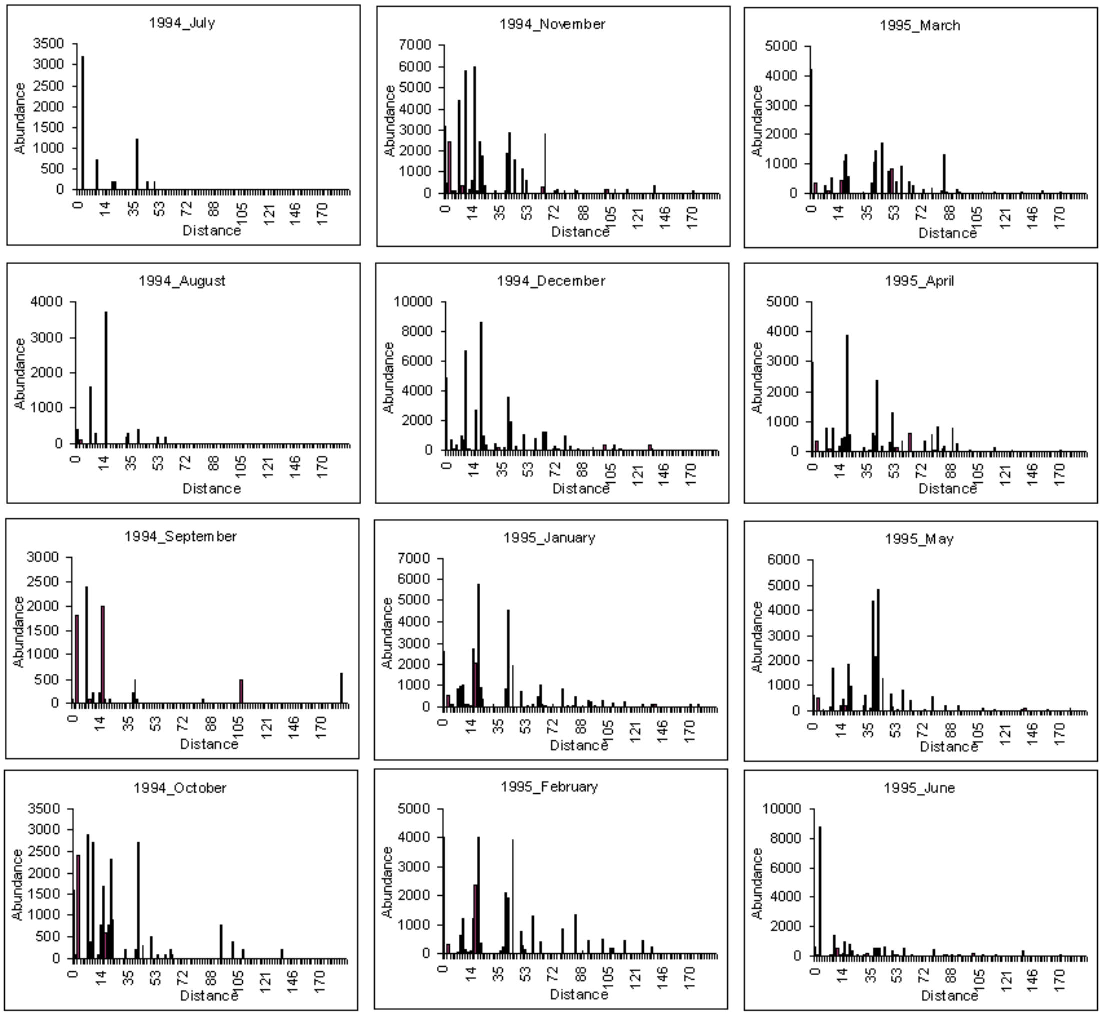


Fig. 14 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1994, starting in July and finishing in June of the following year, 1995.

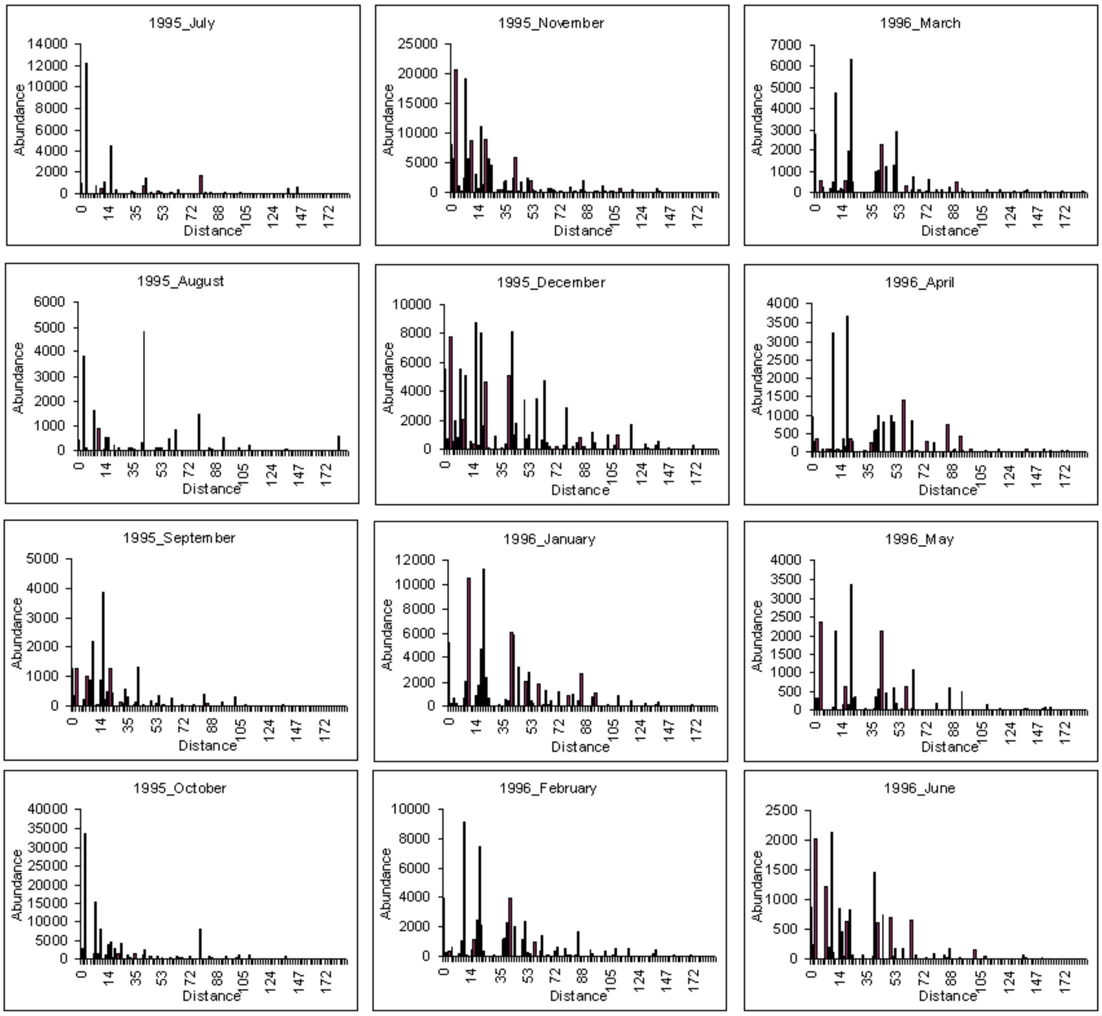


Fig. 15 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1995, starting in July and finishing in June of the following year, 1996.

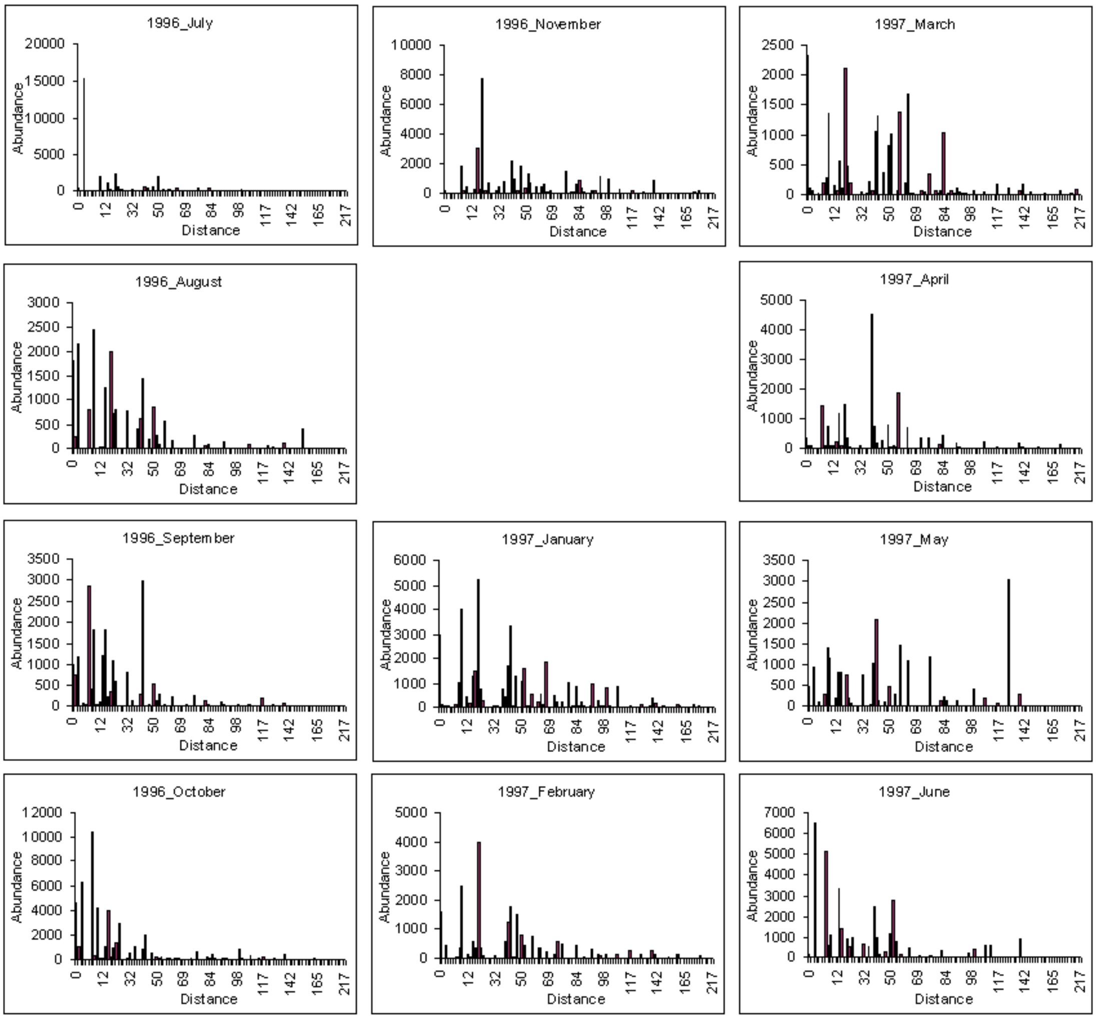


Fig. 16 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1996, starting in July and finishing in June of the following year, 1997, with exception of December.

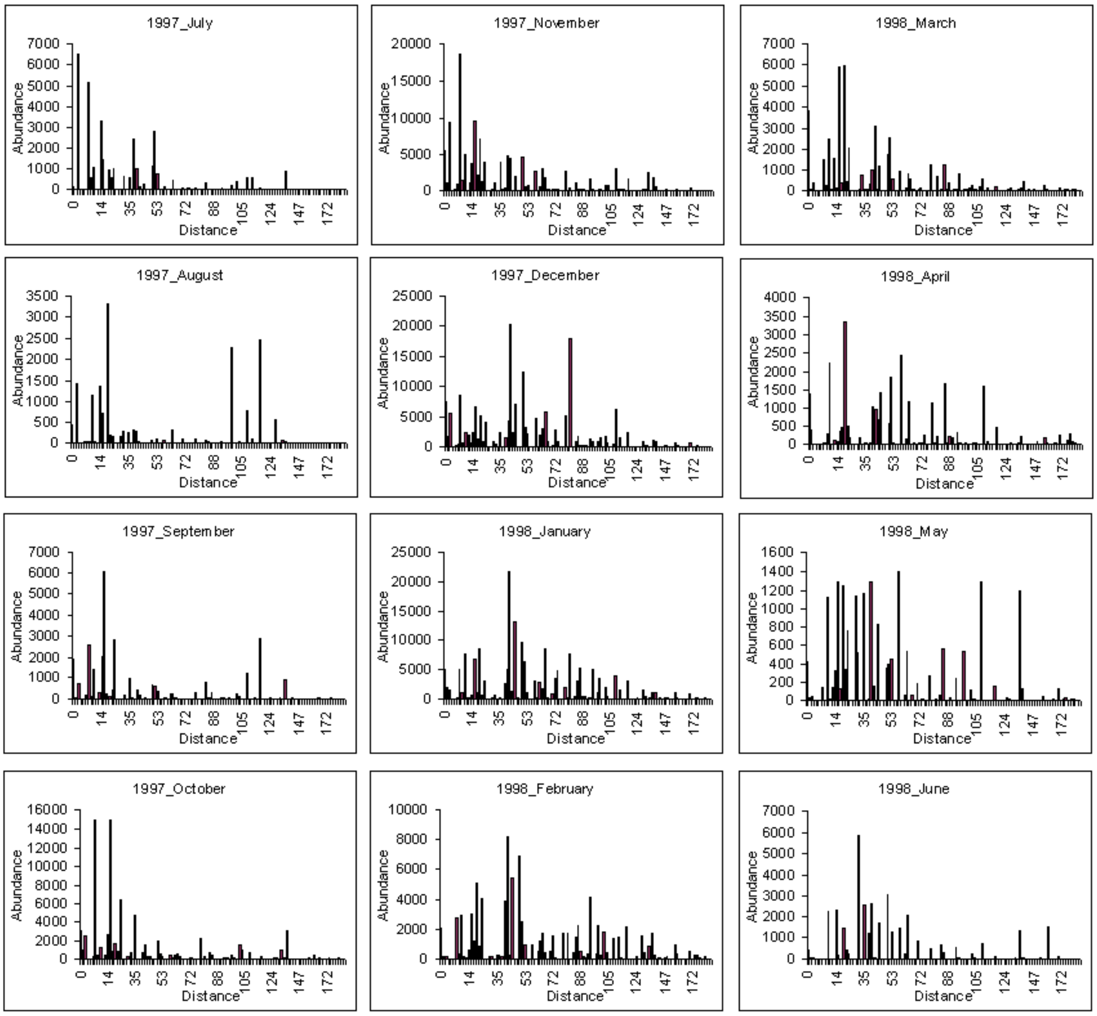


Fig. 17 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1997, starting in July and finishing in June of the following year, 1998.

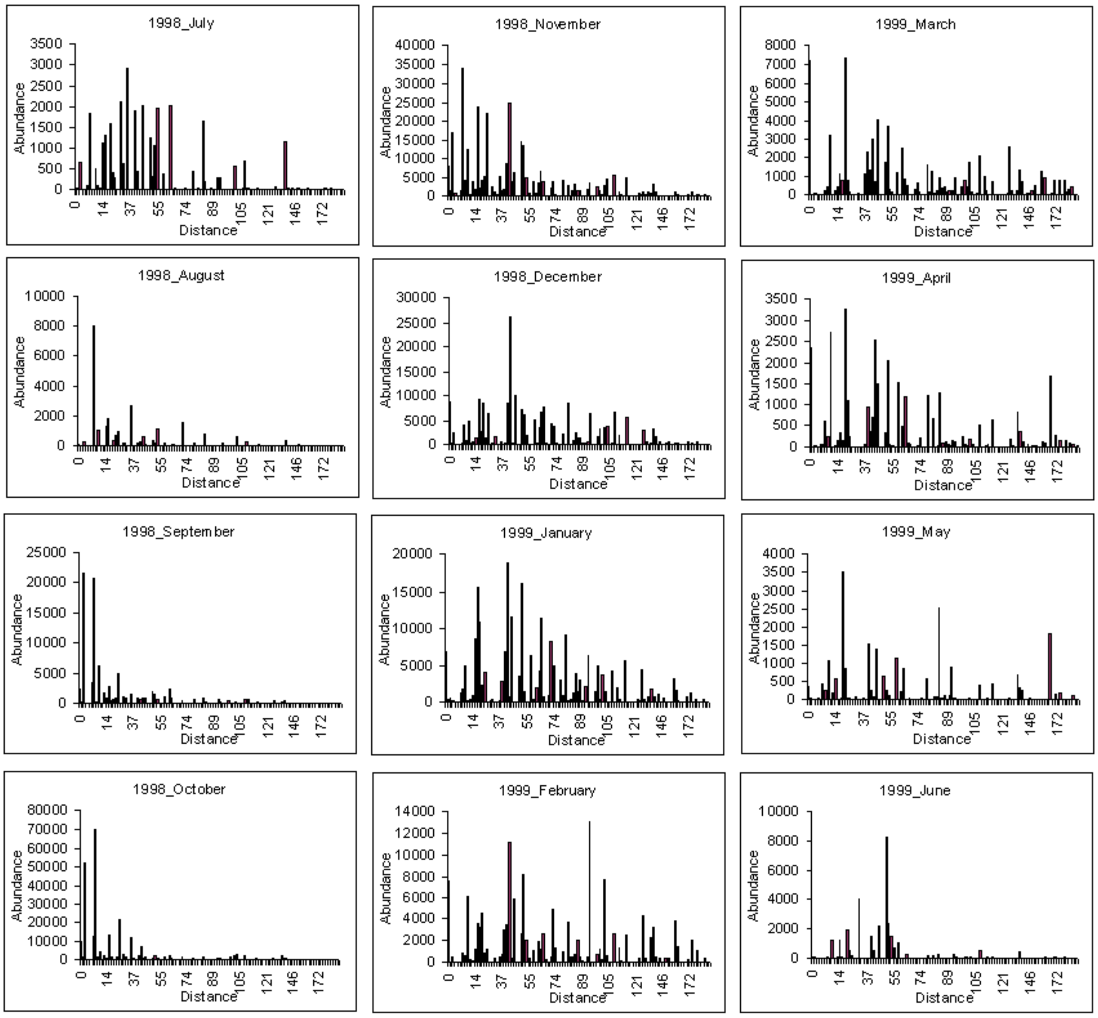


Fig. 18 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1998, starting in July and finishing in June of the following year, 1999.

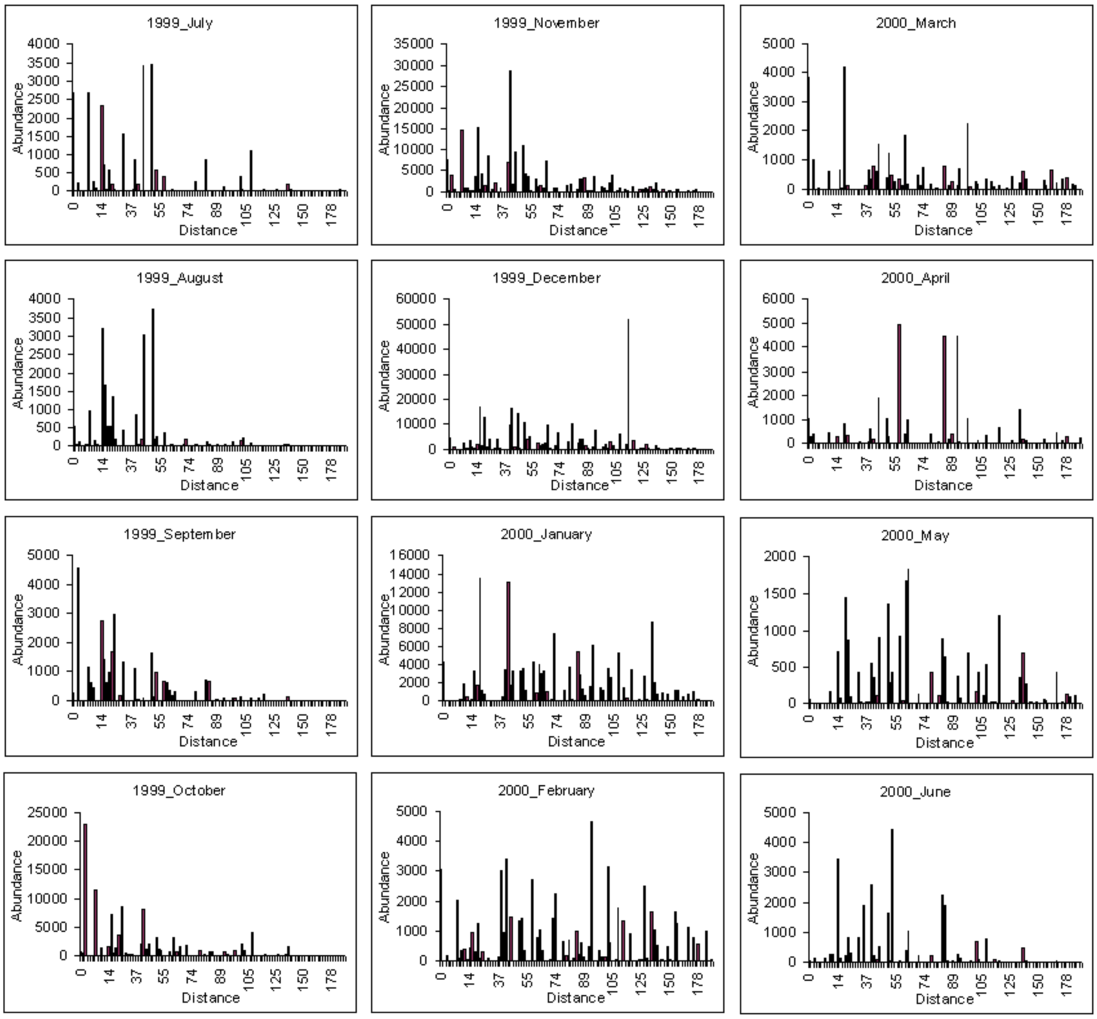


Fig. 19 – Distance to coast (miles) of *L. forbesi* abundance for each month of 1999, starting in July and finishing in June of the following year, 2000.

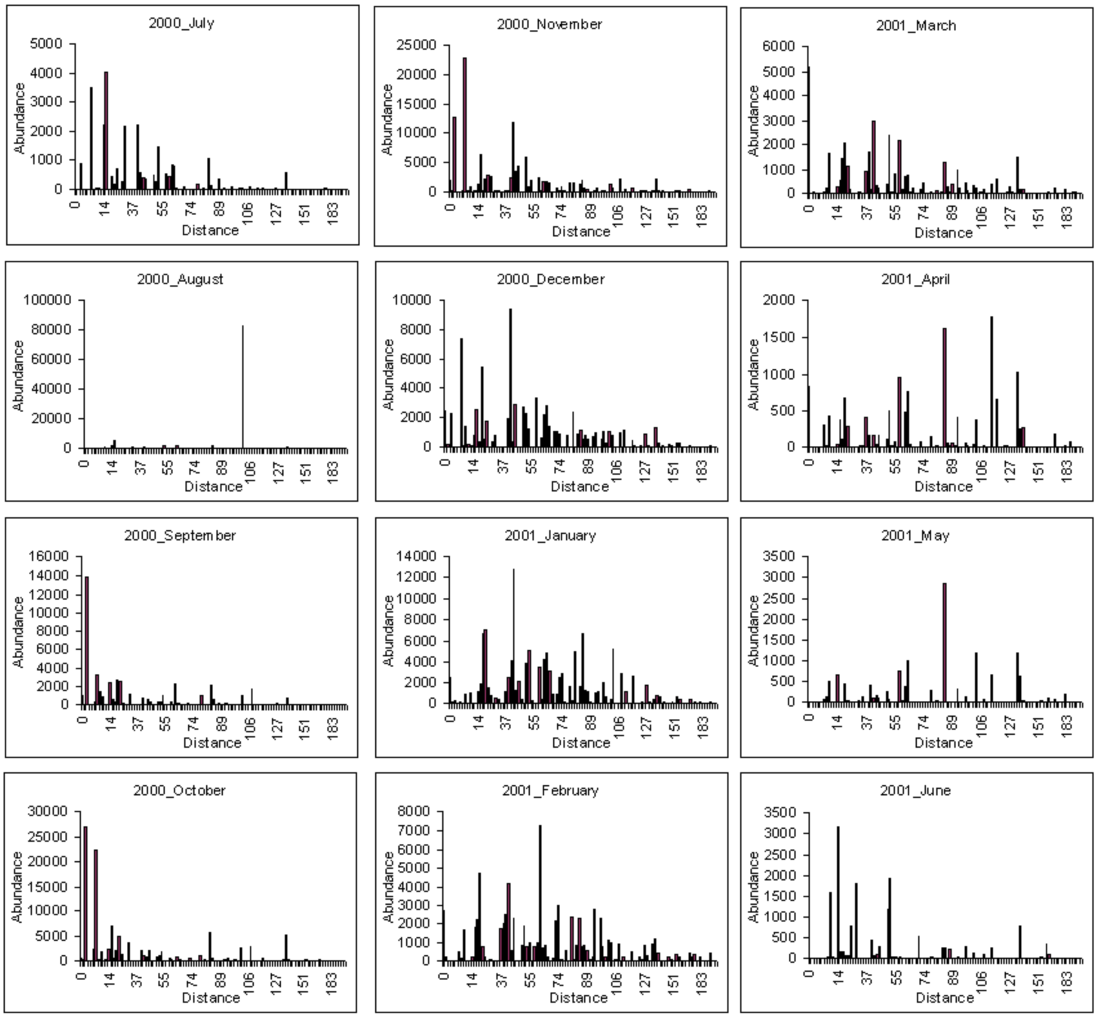


Fig. 20 – Distance to coast (miles) of *L. forbesi* abundance for each month of 2000, starting in July and finishing in June of the following year, 2001.

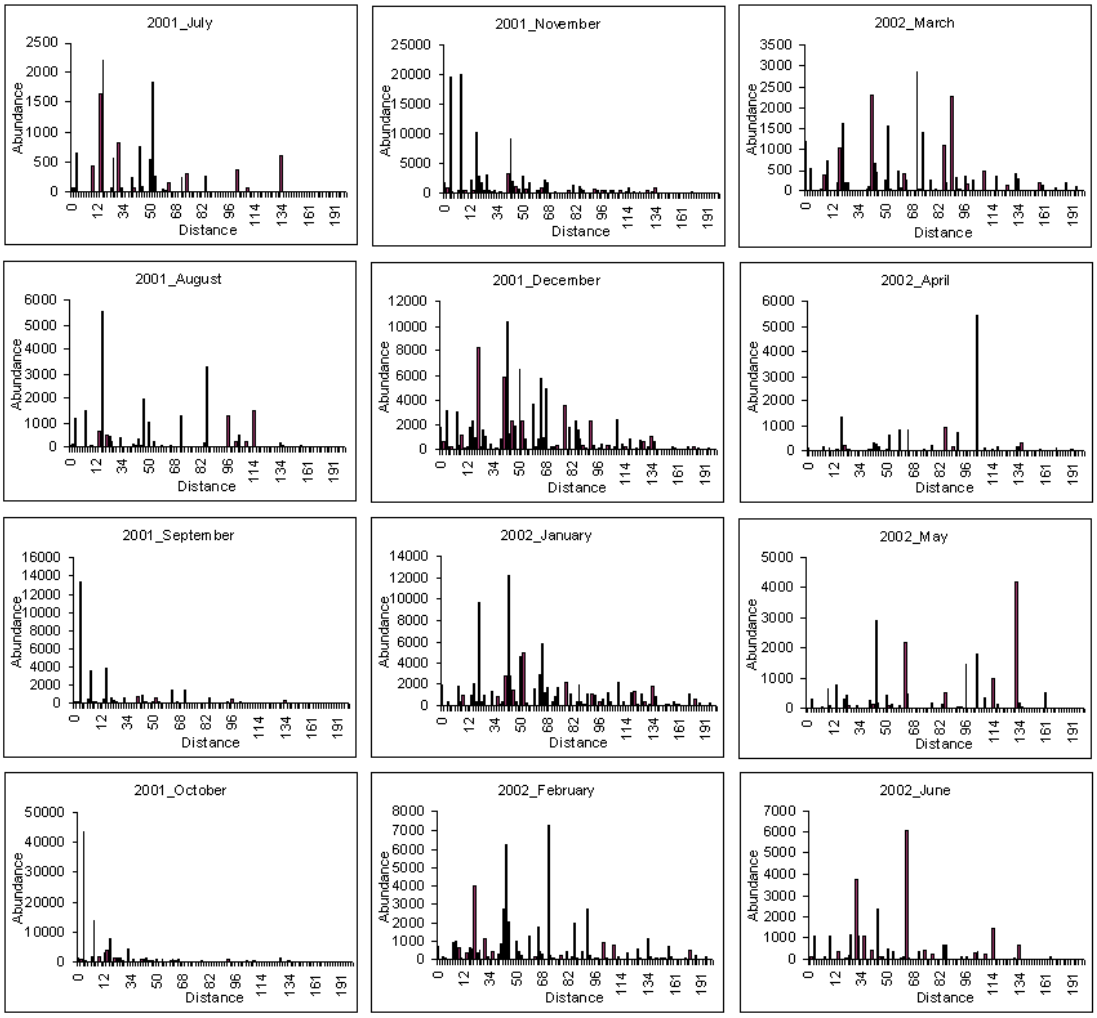


Fig. 21 – Distance to coast (miles) of *L. forbesi* abundance for each month of 2001, starting in July and finishing in June of the following year, 2002.

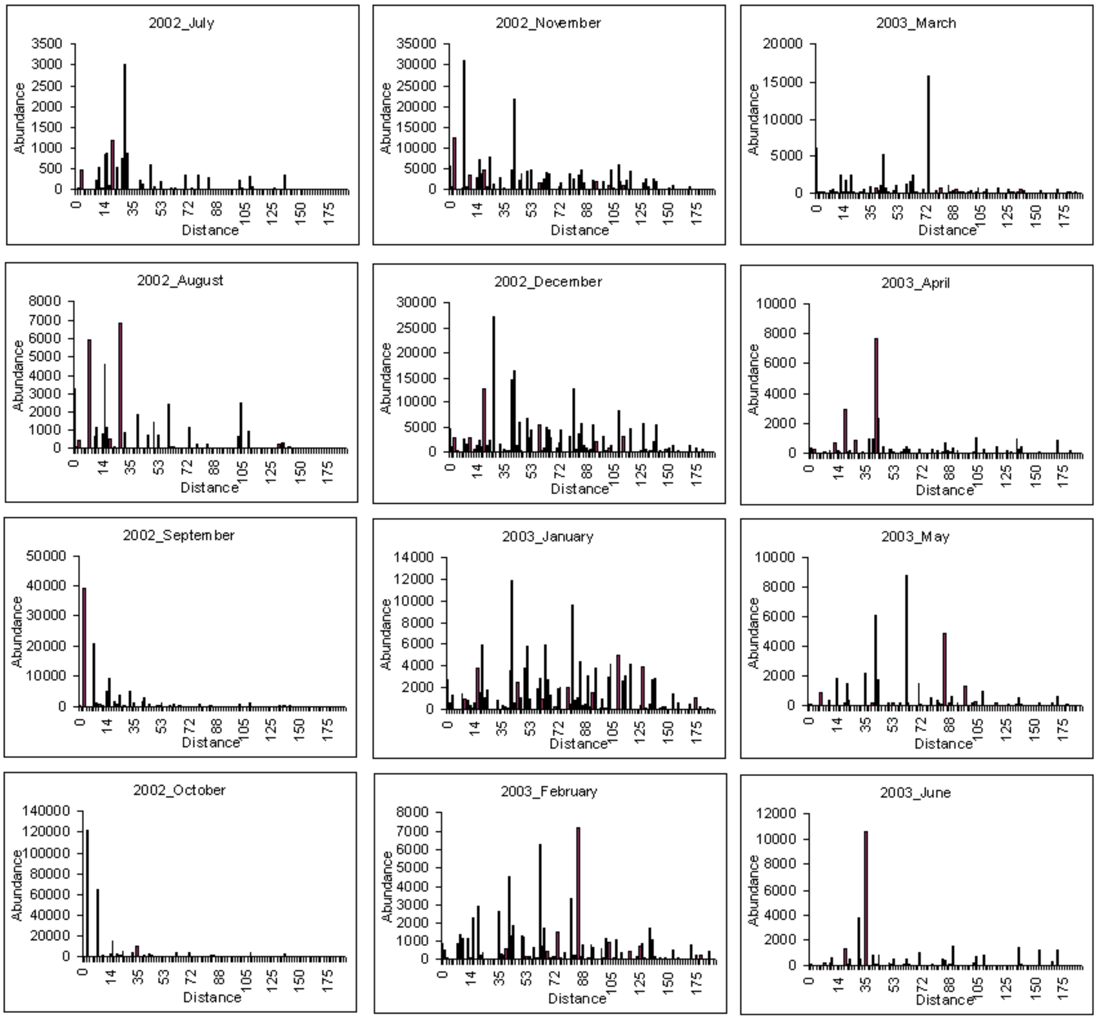
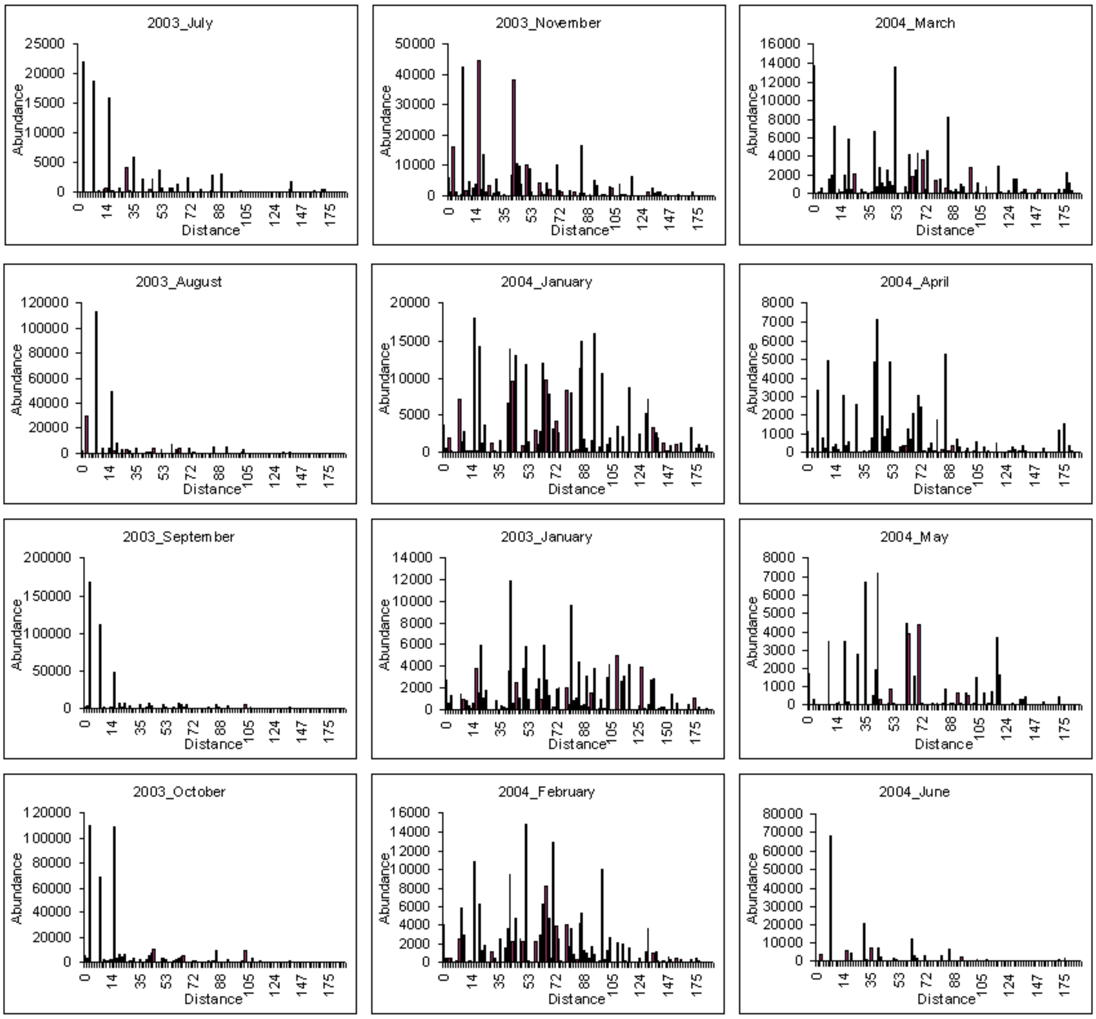


Fig. 22 – Distance to coast (miles) of *L. forbesi* abundance for each month of 2002, starting in July and finishing in June of the following year, 2003.



2003_July

2003_November

2004_March

2003_August

2004_January

2004_April

2003_September

2003_January

2004_May

2003_October

2004_February

2004_June

Fig. 23 – Distance to coast (miles) of *L. forbesi* abundance for each month of 2003, starting in July and finishing in June of the following year, 2004.

Appendix VI – Graphics of the distance of length frequency (class 2, 4 and 6) to coast

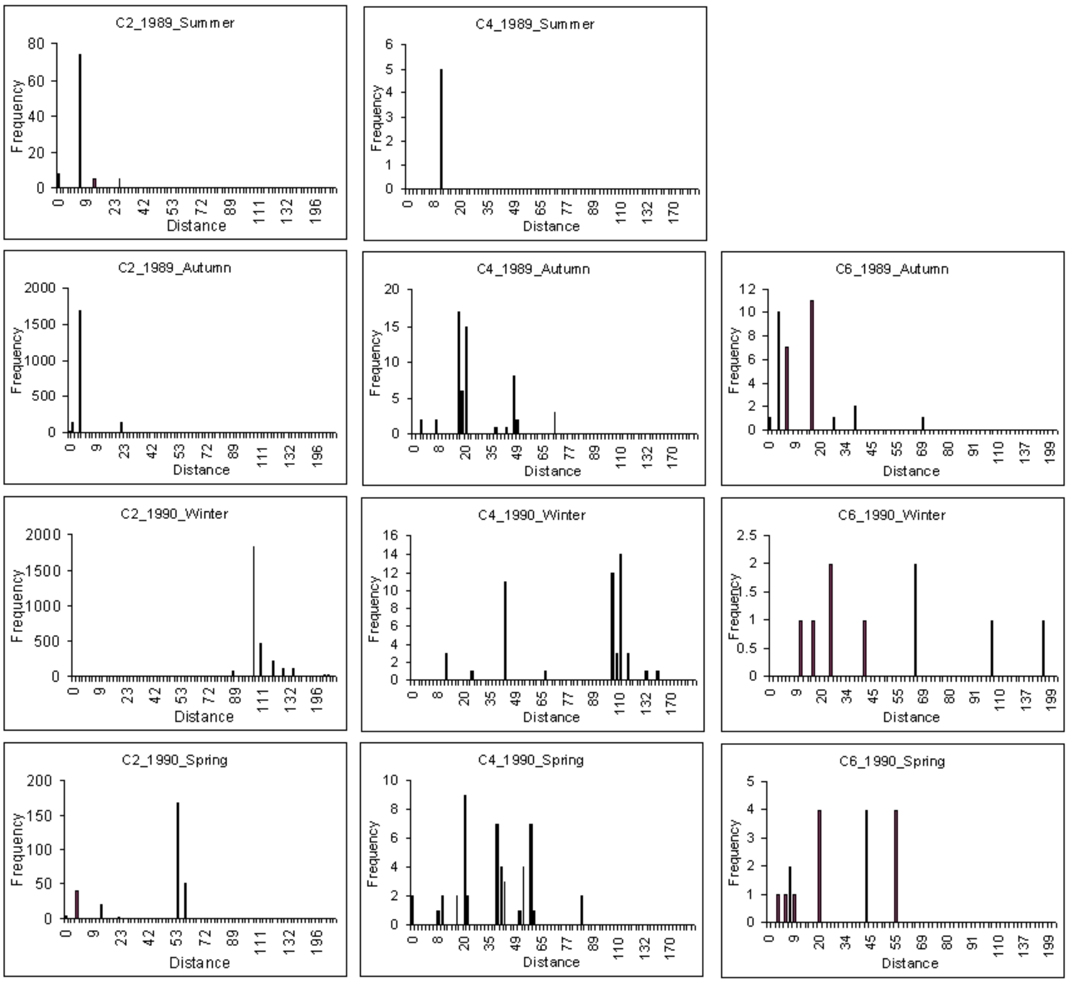
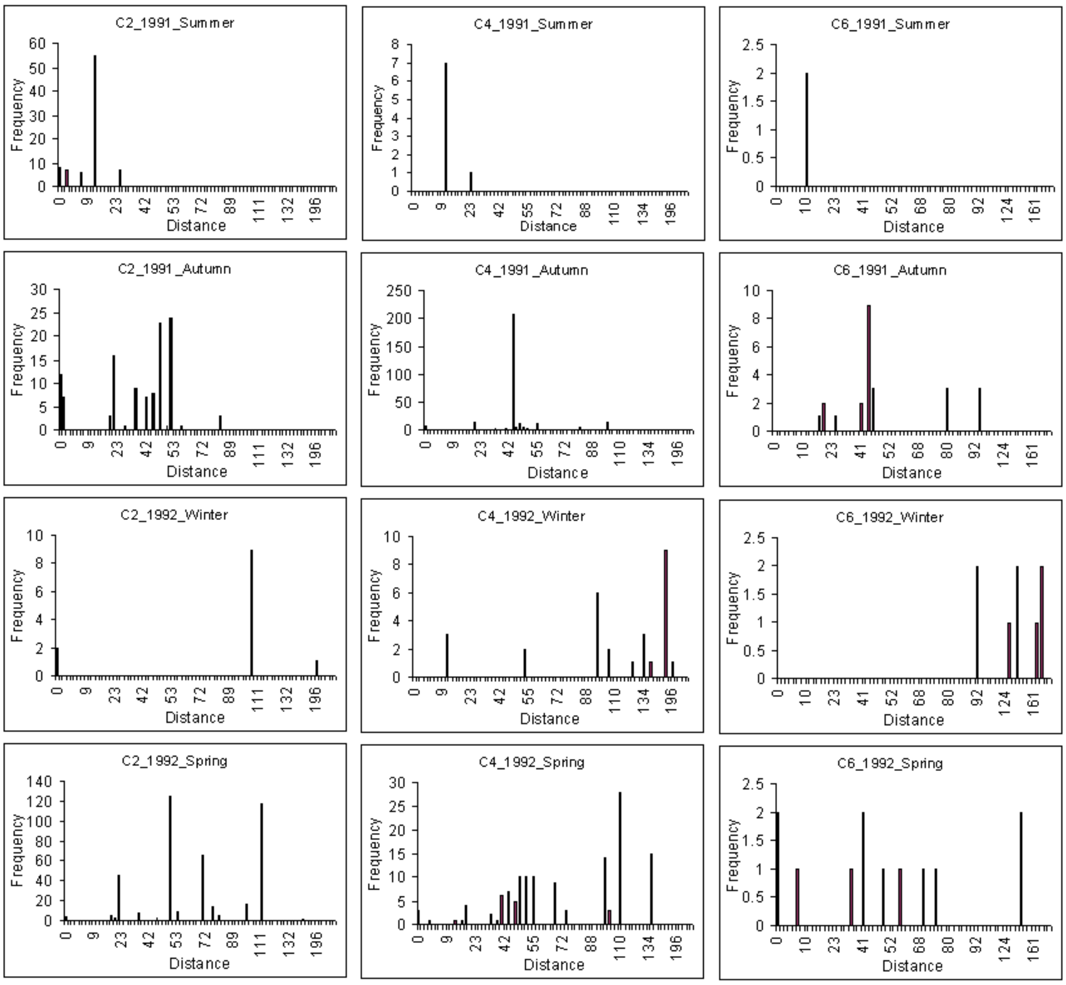


Fig 1. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1989, starting in summer and finishing in spring of the following year, 1990. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.



C2_1991_Summer

C4_1991_Summer

C6_1991_Summer

C2_1991_Autumn

C4_1991_Autumn

C6_1991_Autumn

C2_1992_Winter

C4_1992_Winter

C6_1992_Winter

C2_1992_Spring

C4_1992_Spring

C6_1992_Spring

Fig 2. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1991, starting in summer and finishing in spring of the following year, 1992. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

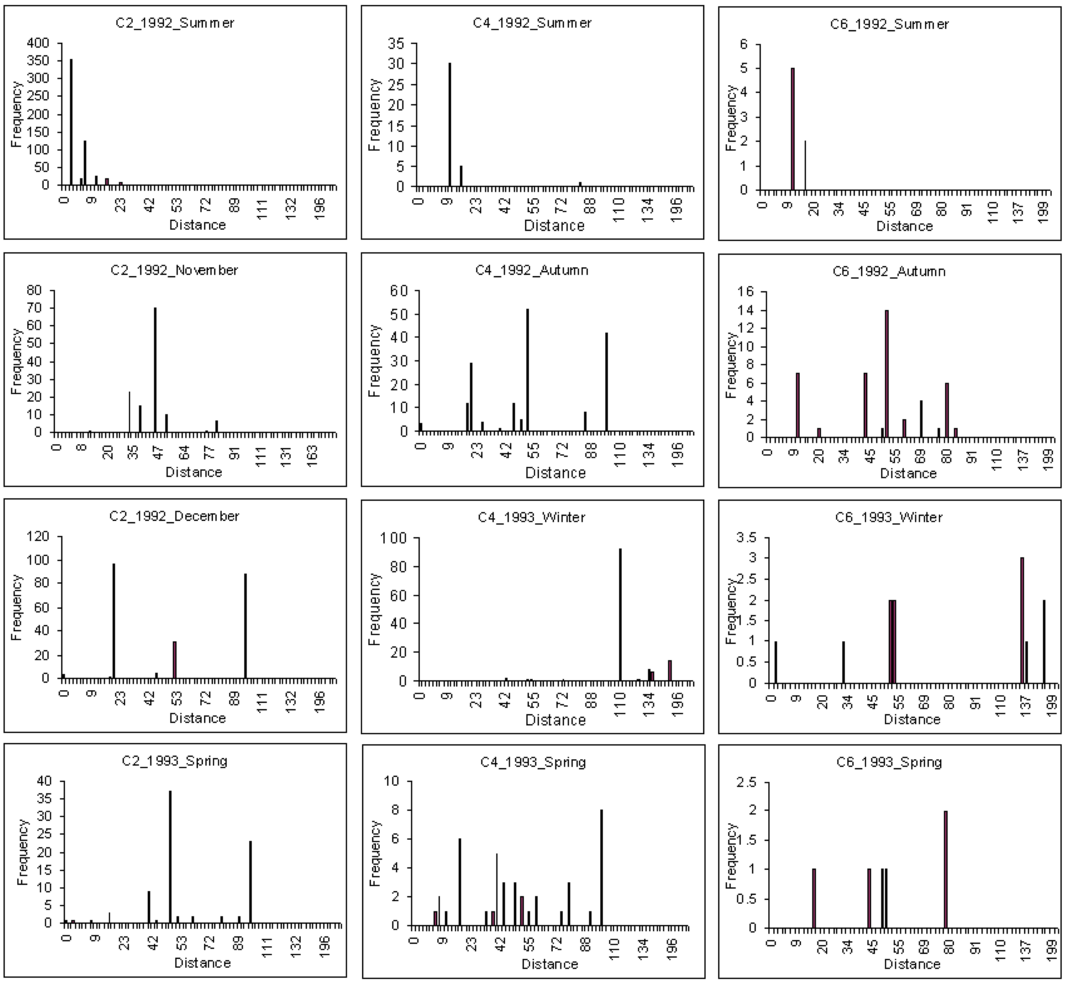


Fig 3. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1992, starting in summer and finishing in spring of the following year, 1992. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

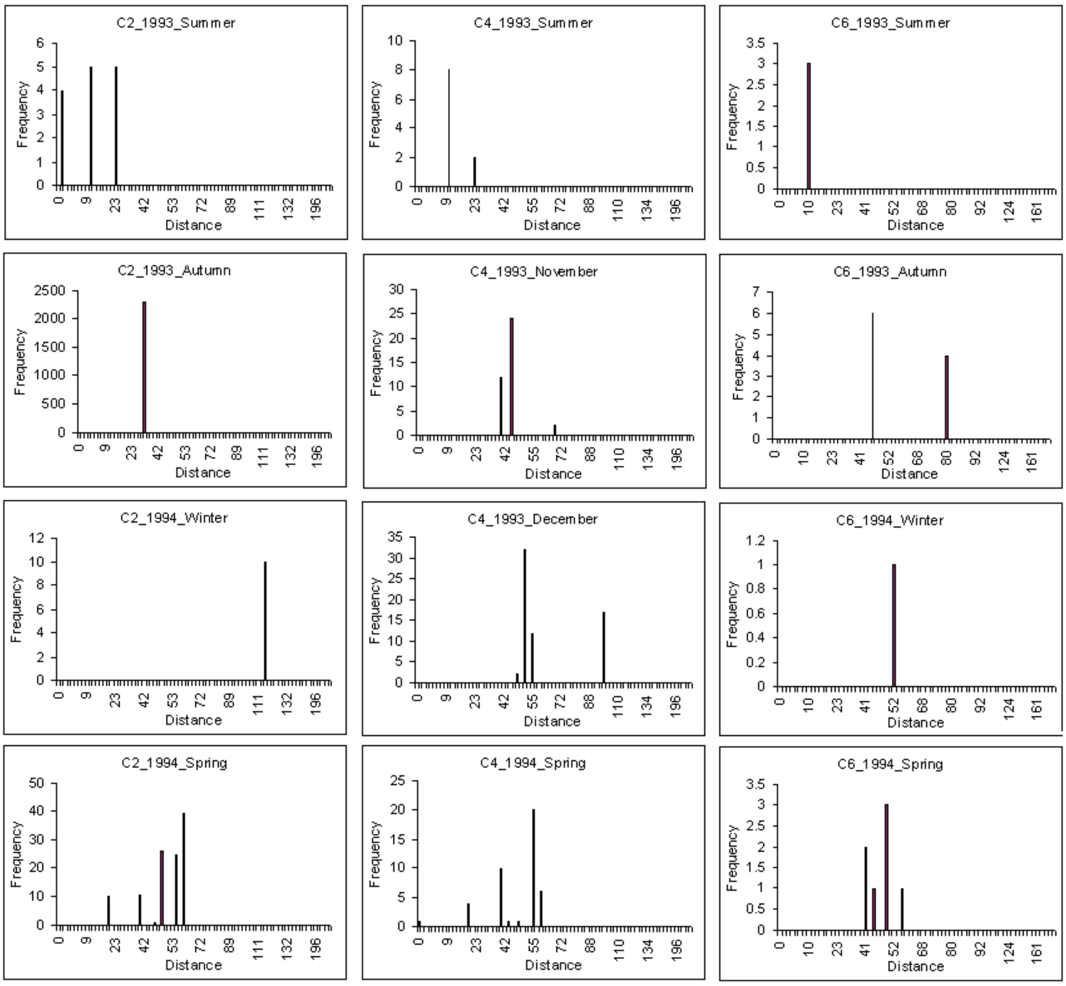


Fig 4. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1993, starting in summer and finishing in spring of the following year, 1994. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

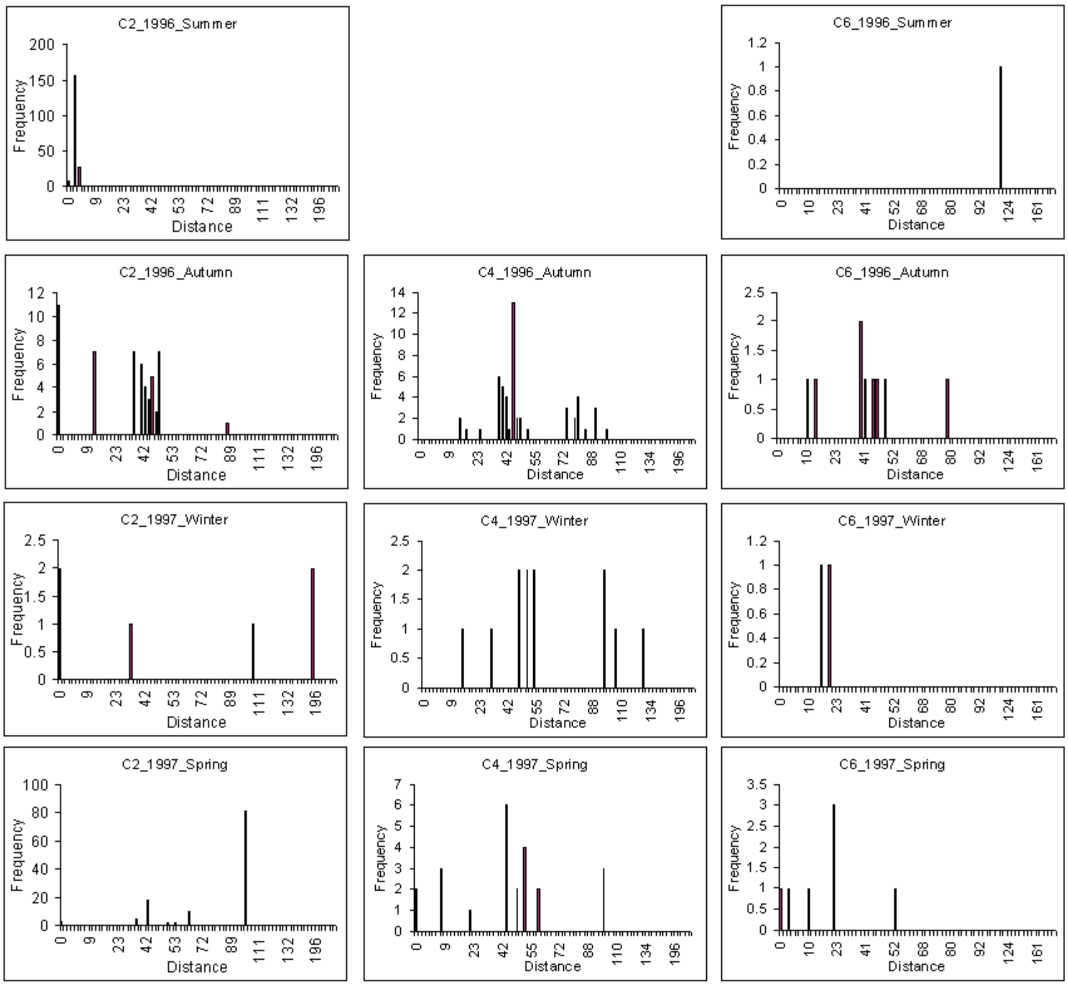


Fig 5. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1996, starting in summer and finishing in spring of the following year, 1997. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

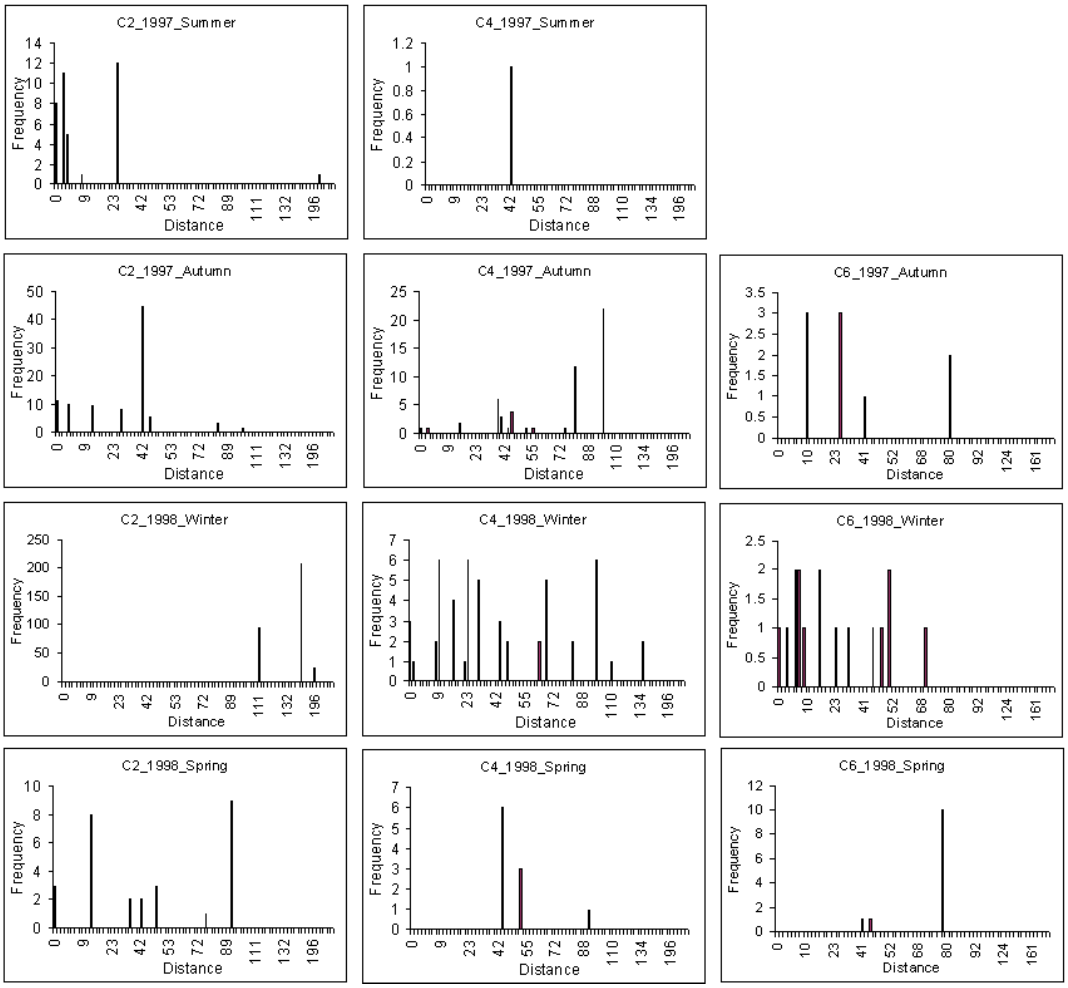


Fig 6. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1997, starting in summer and finishing in spring of the following year, 1998. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

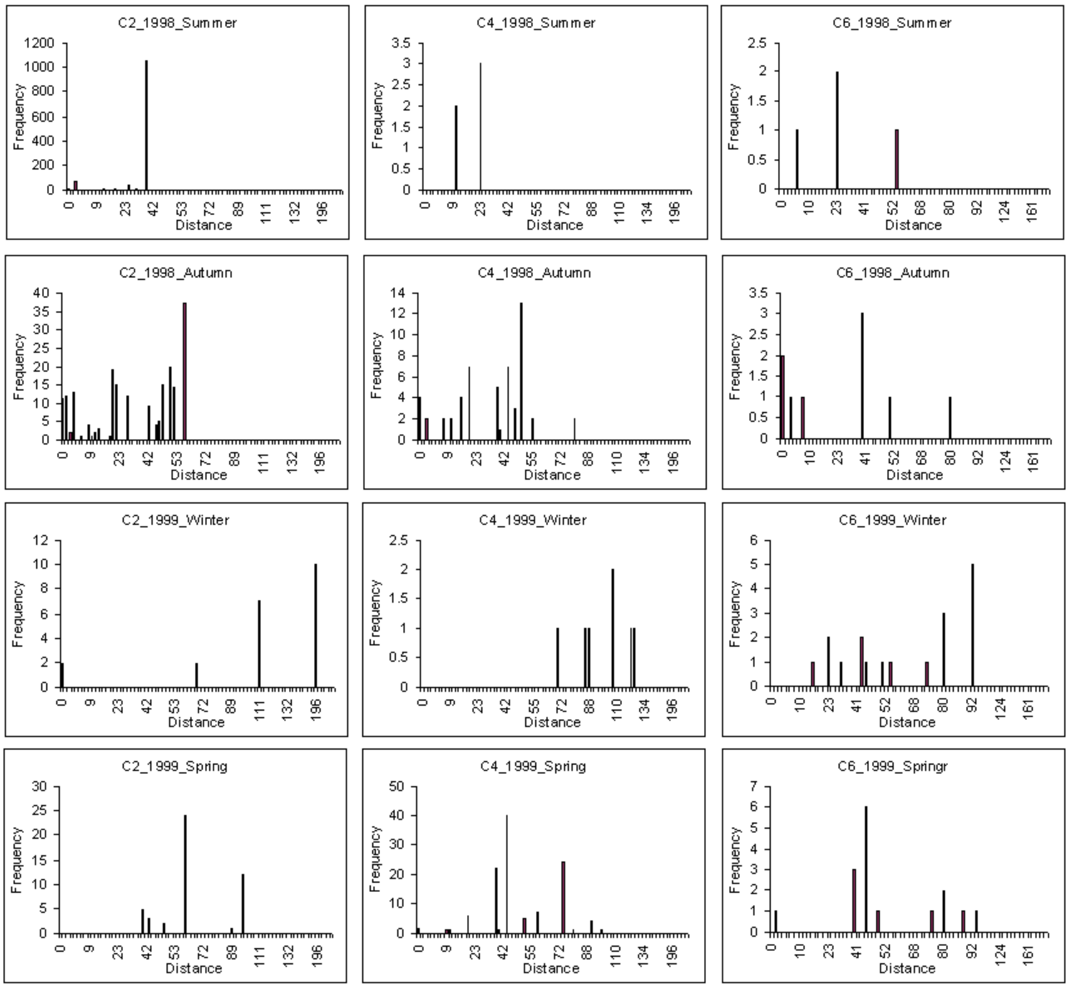


Fig 7. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1998, starting in summer and finishing in spring of the following year, 1999. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

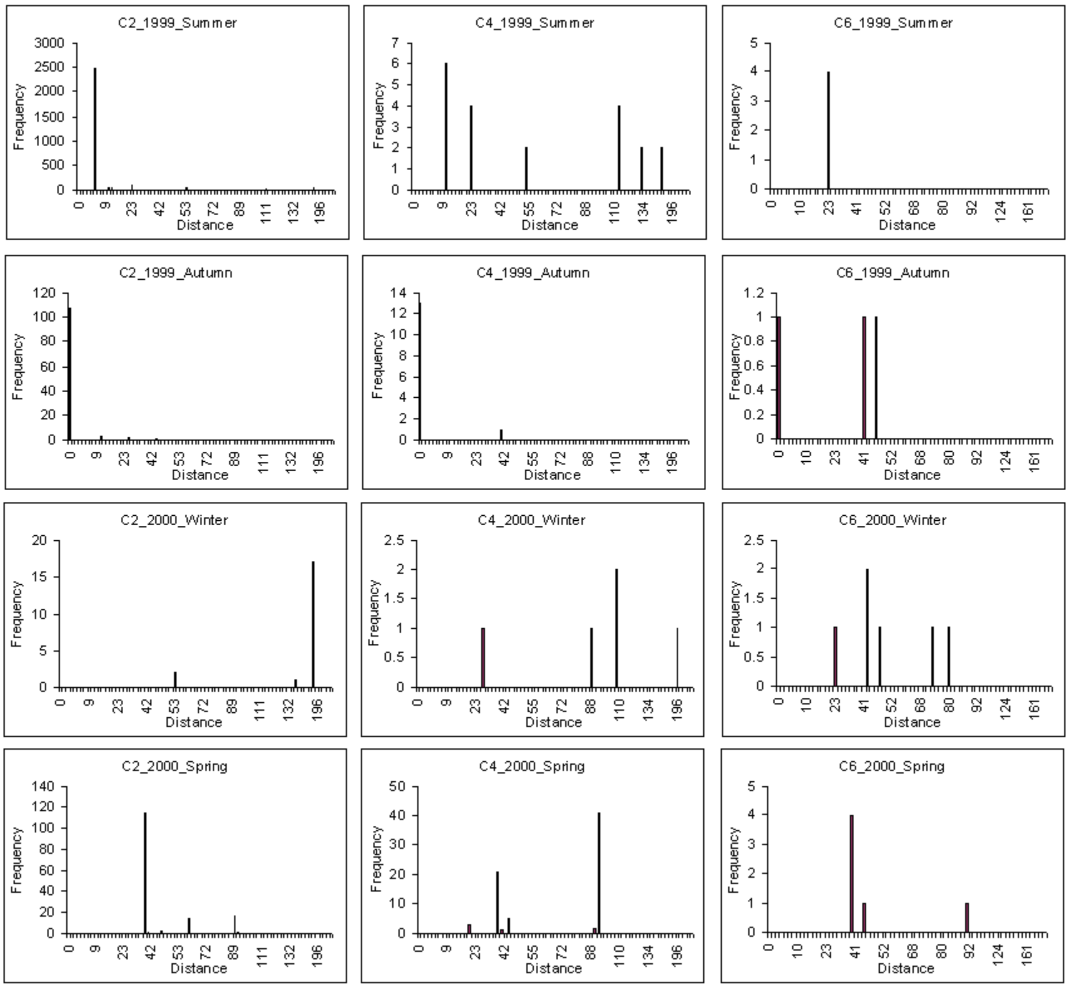


Fig 8. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 1999, starting in summer and finishing in spring of the following year, 2000. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

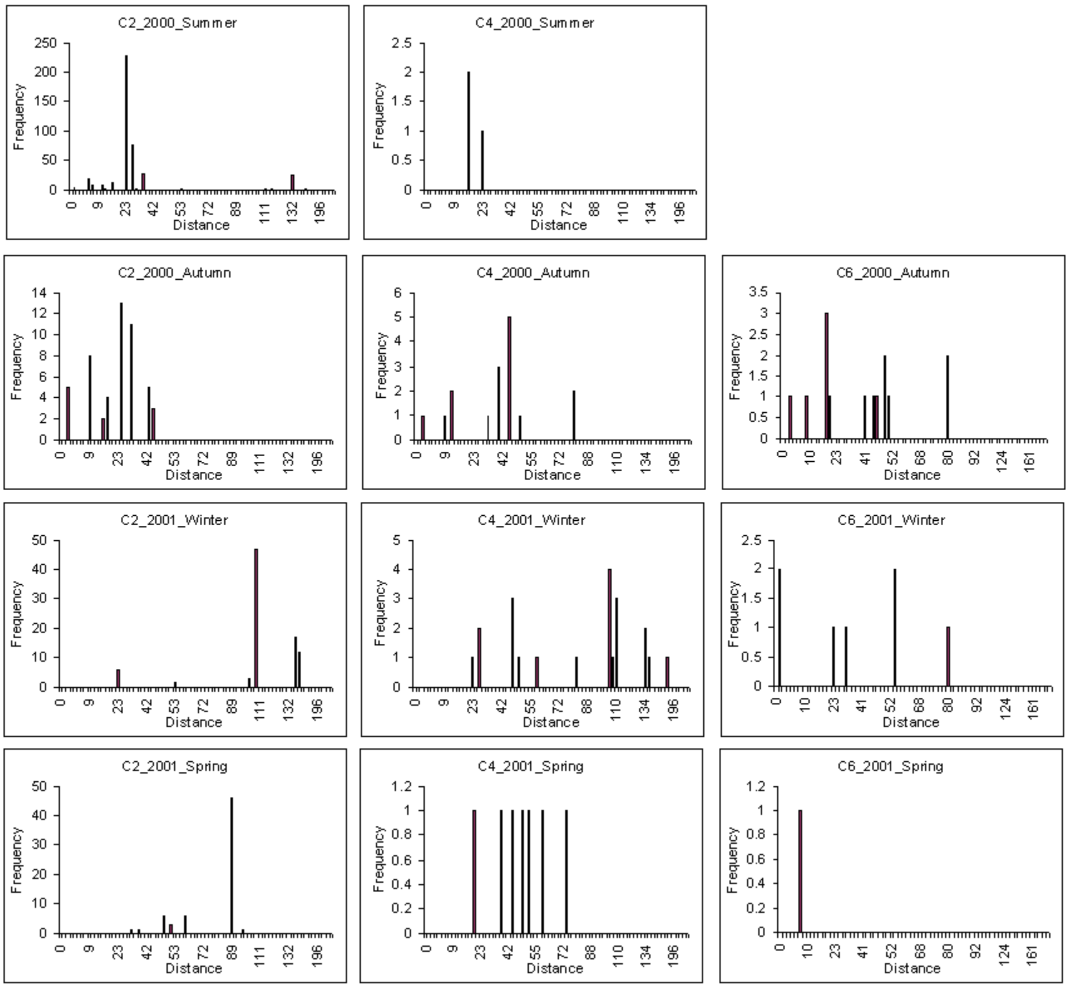


Fig 9. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 2000, starting in summer and finishing in spring of the following year, 2001. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

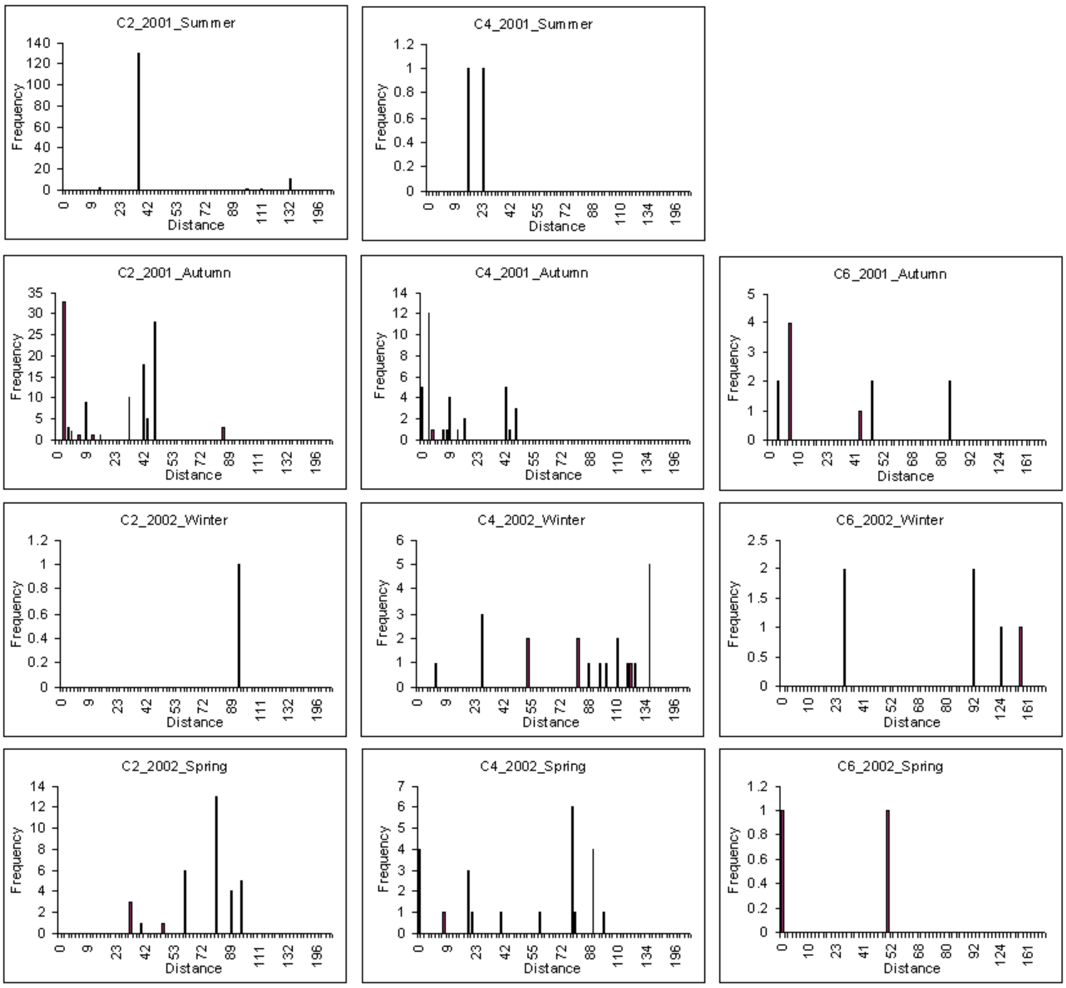


Fig 10. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 2001, starting in summer and finishing in spring of the following year, 2002. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

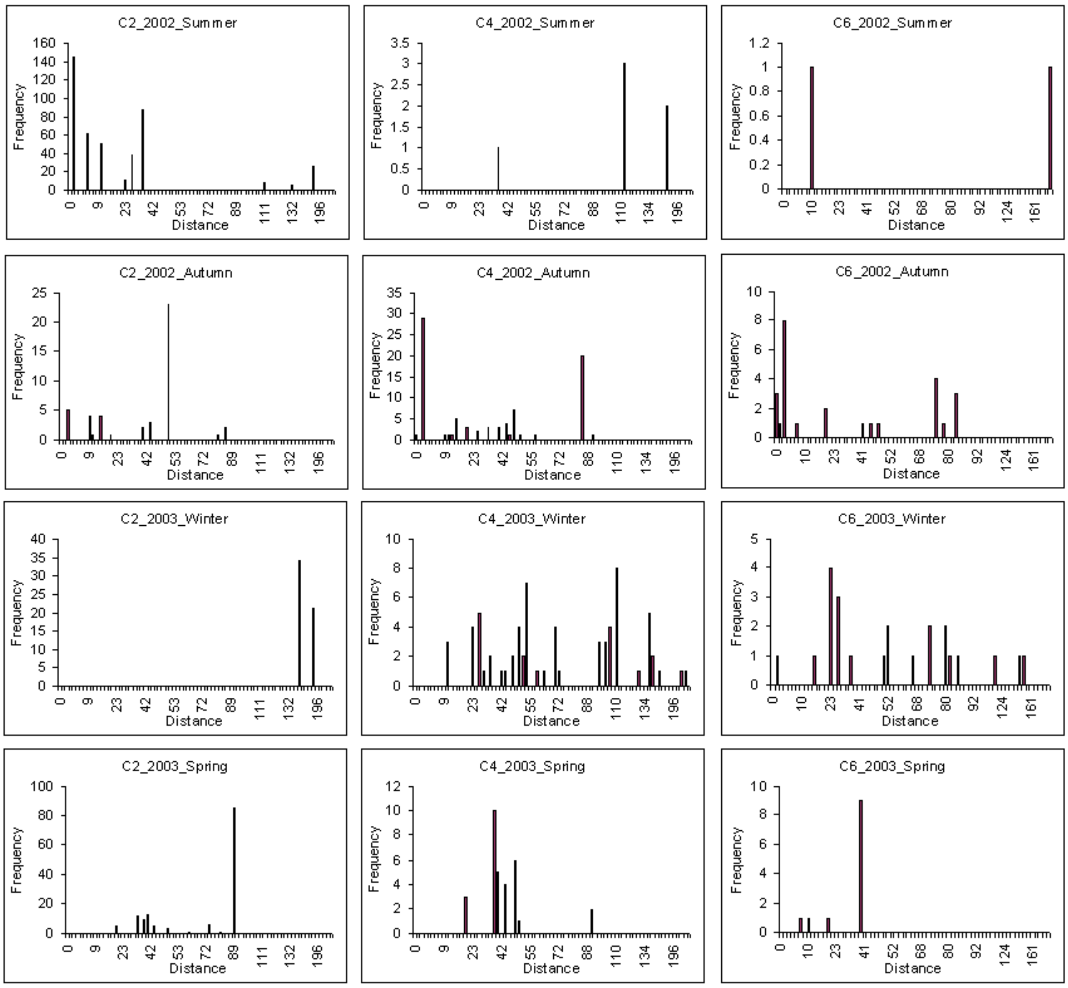


Fig 11. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 2002, starting in summer and finishing in spring of the following year, 2003. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

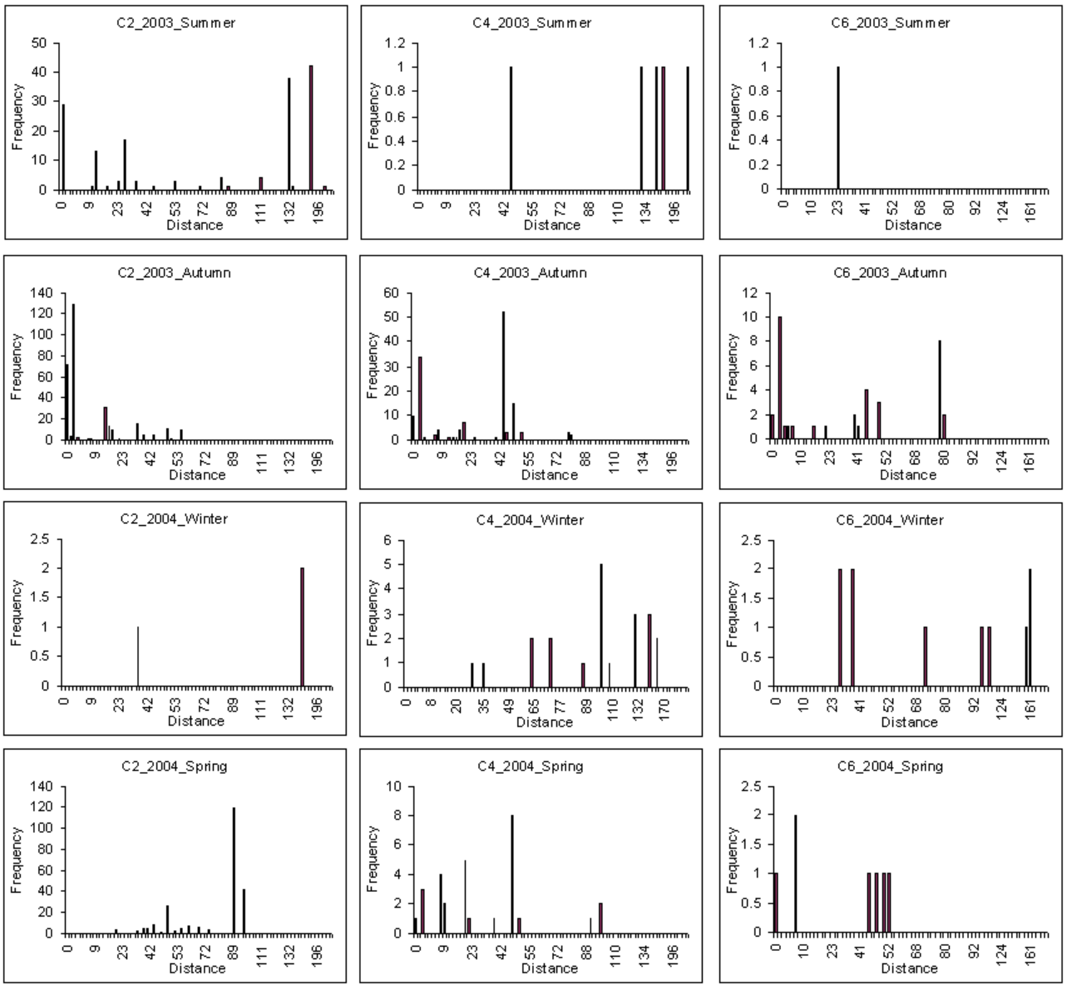


Fig 12. – Distance to coast (miles) of *L. forbesi*, with length class 2 (left), 4 (middle) and 6 (right), occurrence frequency for each season of 2003, starting in summer and finishing in spring of the following year, 2004. Animals of length class 2: 5-9.5cm; length class 4: 15-19cm; length class 6: 25-29cm.

Appendix VII – Smooth curves obtained with GAMM on Model B

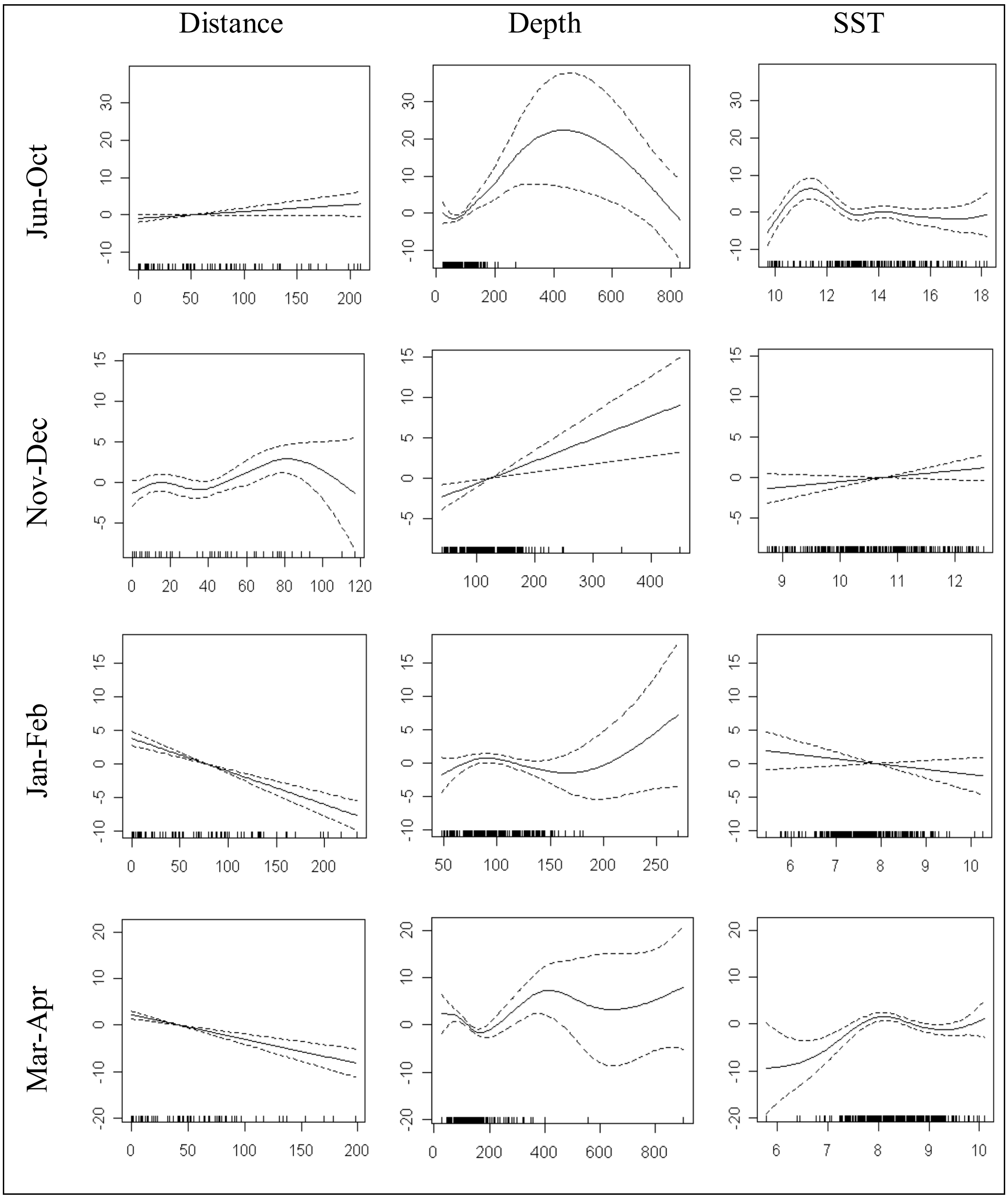


Fig. 1– GAMM smoothing curves of survey data using the average length class of all squid caught in each haul as a response variable. The average length class are represented as a function of the smooth terms, distance to coast (miles), depth (m) and SST (^{o}C) for each season. Dashed lines represent two standard error boundaries around the main affects (95% confidence limits).