



Patterns in the spatial distribution of Peruvian anchovy (*Engraulis ringens*) revealed by spatially explicit fishing data

Sophie Bertrand^{a,b,c,*}, Erich Díaz^b, Matthieu Lengaigne^d

^a University of Washington, School of Aquatic and Fisheries Sciences, Box 355020, Seattle, WA 98195-5020, USA

^b IMARPE, Esquina Gamarra y General Valle S/N, Chuchito, Callao, Lima, Peru

^c Institut de Recherche pour le Développement (IRD), Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France

^d IRD, LOCEAN, Tour 45-55, 4ème Etage, 4 Place Jussieu, 75252 Paris Cedex 05, France

ARTICLE INFO

Article history:

Accepted 14 October 2008

Available online 21 October 2008

Keywords:

Peruvian anchovy

Fish distribution

Vessel monitoring system (VMS)

Neural network

Multilayer perceptron (MLP)

Fishing sets distribution

Clustering index

Purse-seine fleet

ABSTRACT

Peruvian anchovy (*Engraulis ringens*) stock abundance is tightly driven by the high and unpredictable variability of the Humboldt Current Ecosystem. Management of the fishery therefore cannot rely on mid- or long-term management policy alone but needs to be adaptive at relatively short time scales. Regular acoustic surveys are performed on the stock at intervals of 2 to 4 times a year, but there is a need for more time continuous monitoring indicators to ensure that management can respond at suitable time scales. Existing literature suggests that spatially explicit data on the location of fishing activities could be used as a proxy for target stock distribution. Spatially explicit commercial fishing data could therefore guide adaptive management decisions at shorter time scales than is possible through scientific stock surveys. In this study we therefore aim to (1) estimate the position of fishing operations for the entire fleet of Peruvian anchovy purse-seiners using the Peruvian satellite vessel monitoring system (VMS), and (2) quantify the extent to which the distribution of purse-seine sets describes anchovy distribution. To estimate fishing set positions from vessel tracks derived from VMS data we developed a methodology based on artificial neural networks (ANN) trained on a sample of fishing trips with known fishing set positions (exact fishing positions are known for approximately 1.5% of the fleet from an at-sea observer program). The ANN correctly identified 83% of the real fishing sets and largely outperformed comparative linear models. This network is then used to forecast fishing operations for those trips where no observers were onboard. To quantify the extent to which fishing set distribution was correlated to stock distribution we compared three metrics describing features of the distributions (the mean distance to the coast, the total area of distribution, and a clustering index) for concomitant acoustic survey observations and fishing set positions identified from VMS. For two of these metrics (mean distance to the coast and clustering index), fishing and survey data were significantly correlated. We conclude that the location of purse-seine fishing sets yields significant and valuable information on the distribution of the Peruvian anchovy stock and ultimately on its vulnerability to the fishery. For example, a high concentration of sets in the near coastal zone could potentially be used as a warning signal of high levels of stock vulnerability and trigger appropriate management measures aimed at reducing fishing effort.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

The Peruvian pelagic ecosystem is highly dominated by anchovy (*Engraulis ringens*). This species sustains the world's largest single species fishery with 6.5 millions tons landed per year on average over the last decade. Management of the fishery presents a unique challenge as anchovy stock dynamics are tightly driven by the high and unpredictable variability of the Humboldt Current Ecosystem (Alheit and Niquen, 2004). Successful management can-

not rely on mid- or long-term policies but needs to be adaptive on weekly or monthly time scales. Decisions on catch and effort limitations within this adaptive management framework need to be based on almost continuous, near real-time estimates of the fish stock condition (available biomass and vulnerability to the fleet), which depend largely on how the fish population is distributed in space (Csirke, 1989; Arreguín-Sánchez, 1996; Harley et al., 2001). Regular scientific acoustic surveys of Peruvian anchovy are performed 2 to 4 times a year by the Instituto del MAR del PERU (IMARPE). To obtain estimates of the condition of the stock at the shorter time steps needed to implement an adaptive management framework, complementary monitoring indicators based on proxies are required.

* Corresponding author. Address: IRD, Teruel 357, Miraflores, Casilla 18-1209, Lima 18, Peru. Tel./fax: +51 1 441 32 23.

E-mail address: Sophie.Bertrand@ird.fr (S. Bertrand).

Existing literature suggests that the spatial distribution of fishing operations should reflect to some extent patterns of fish distribution. Fishers constitute, with marine birds and sea lions (Muck and Pauly, 1987; Muck and Fuentes, 1987), the main predators of the Peruvian anchovy population. Although predator–prey spatial relationships may be complex (Fauchald et al., 2000; Davoren et al., 2002), fishers have to search for and find their prey, and their spatial behaviour track the dynamics of prey distribution in a similar way to animal predators (Frontier, 1987; Russel et al., 1992; Bertrand et al., 2005, 2007). Peruvian anchovy are targeted primarily by purse-seiners. Fishing set locations are currently known for a small fraction of the fleet (about 1.5% of the vessels) from an at-sea observer program run by IMARPE. Continuous monitoring of vessel location is obtained via a satellite vessel monitoring system (VMS) called SISESAT (Sistema de SEguimiento SATelital). Implemented in 1999, SISESAT covers the movements of the entire industrial anchovy fishery (approximately 1350 fishing vessels), providing high resolution, real-time, and low cost information on fleet behaviour and spatial dynamics. In this study our aim is to estimate fishing set locations from the one-dimensional geometry of the vessel path provided by the raw VMS data, and to assess the extent to which these estimates are representative of the distribution of anchovy along the Peruvian coast.

A growing number of studies have made use of satellite VMS data to better understand fishery dynamics and behaviour (Bertrand et al., 2005; Bertrand et al., 2007; Deng et al., 2005; Dinmore et al., 2003; Mills et al., 2007; Murawski et al., 2005). In the Peruvian anchovy fishery, purse-seiners fitted with VMS automatically report their position once an hour or less on average. VMS data do not explicitly report whether a vessel is fishing. Each fishing trip lasts from a few hours to 2 days, and one fishing operation (set) lasts on average 2 h. In the course of a fishing trip, between one and five fishing operations may occur on average. Because the time taken for a fishing set is only twice that of the VMS sampling period, identifying fishing set locations from VMS is possible but not trivial. Speed-related criteria have been trialled

(speed usually ranges between 0.2 and 1.6 knots, i.e. 0.4–2.9 km h⁻¹, during a fishing set) but tend to over-estimate the number of fishing sets (+182%) due to similarities in vessel speeds when fishing, drifting, and searching.

To improve identification performance, we implement an identification methodology based on artificial neural networks (ANN, Bishop, 1995; Ripley, 1996; Fine, 1999) which have recently become popular tools for non-parametric classification and prediction in many fields of science and engineering. ANNs have proven to be successful at modelling a number of fishery-related variables and to outperform comparable linear models for Pacific herring (*Clupea pallasii*) recruitment (Chen and Ware, 1999), for modelling of virtual fishermen searching behaviour (Dreyfus-León, 1999), and for predicting the relative abundance of bigeye tuna (*Thunus obesus*) from catch and effort data (Maunder and Hinton, 2006) for instance. In this study, we developed an ANN fed with raw VMS data and trained on a sample of fishing trips with known fishing set positions (provided by at-sea observers) to predict a binary response (fishing set/no fishing set). Fishing set positions estimated by the ANN were then compared with acoustic data estimating anchovy biomass to determine the extent to which the spatial distribution of the fleet fishing operations correlates with the patterns displayed by the anchovy stock.

2. Material and methods

2.1. Data

VMS data used to identify fishing set locations were extracted from the SISESAT database, which contains vessel movements for the entire industrial anchovy fleet (about 1350 vessels) since 1999. Each vessel is equipped with an Argos satellite transmitter and global positioning system (GPS) receiver. The transmitter sends a time-referenced position with an accuracy of 100 m on an hourly basis. VMS data extracted from the database covered all of the fishing seasons between 2000 and 2002 (22 months,

Table 1
Summary of the study periods, the corresponding number of fishing sets and elementary sampling distance units (ESDU), and the different indexes computed for describing fish and fishing sets distributions: mean distance to the coast (MDC), total area of the convex polygon enclosing the distribution (TA) and clustering index (Clust).

Month fishing operations	Num fishing sets	MDC (km)	TA (km ²)	Clust.(km ²)	Acoustic survey reference	Date of the survey in the study zone	Number of ESDU		MDC (km)	TA (km ²)	Clust. (km ²)
							S _A > 0	S _A > 500			
March 2000	2376	49.5	39,115	63,323	Sv 2000 01–02	09/02–20/02	1451	765	89.3	73,589	32,985
April 2000	997	61.4	40,332	54,343	–	–	–	–	–	–	–
May 2000	1648	52.4	31,023	55,633	–	–	–	–	–	–	–
June 2000	1592	55.6	53,898	73,026	–	–	–	–	–	–	–
July 2000	2801	80.1	56,713	153,481	Sv 2000 06–07	10/06–22/06	741	131	91.9	82,664	175,378
October 2000	1058	18.9	25,055	279,410	Sv 2000 08–09	30/08–12/09	551	113	23.7	66,022	132,648
November 2000	1902	23.9	39,235	79,306	Sv 2000 10–11	16/10–24/10	646	81	28.7	60,864	113,667
December 2000	1703	79.7	37,190	102,379	–	–	–	–	–	–	–
April 2001	1590	55.4	32,131	61,265	Sv 2001 02–04	09/03–18/03	961	514	60.2	50,317	37,050
June 2001	3455	41.0	45,299	26,836	–	–	–	–	–	–	–
July 2001	172	32.8	40,696	77,077	Sv 2001 07–08	11/07–20/07	824	116	70.9	52,899	64,472
October 2001	760	19.1	7 738	64,026	Sv 2001 08–09	30/08–14/09	622	133	18.9	49,442	122,406
November 2001	208	18.0	5 632	191,618	Sv 2001 10–11*	–	–	–	–	–	–
December 2001	129	18.7	10,691	34,618	–	–	–	–	–	–	–
March 2002	1287	31.5	7 851	123,525	–	–	–	–	–	–	–
April 2002	2512	48.2	29,850	39,015	Sv 2002 02–03	01/03–10/03	619	337	40.4	37,105	36,858
May 2002	2880	48.2	33,771	82,736	–	–	–	–	–	–	–
June 2002	1635	77.6	40,487	57,118	–	–	–	–	–	–	–
July 2002	1662	88.4	43,769	170,898	Sv 2002 08	17/08–27/08	679	110	82.8	64,523	135,481
October 2002	407	77.0	28,797	73,383	–	–	–	–	–	–	–
November 2002	3512	58.1	31,439	165,164	Sv 2002 10–11	25/10–09/11	631	99	41.1	53,925	72,227
December 2002	4088	20.5	14,711	155,632	–	–	–	–	–	–	–

* One survey performed during 10–11 2001 was discarded because an important bias between sampling by acoustic and by the fishery was evidenced by IMARPE at this period.

see Table 1 for details) and Peruvian coastal waters from 7°S to 10°S (Fig. 1). SISESAT does not make the distinction between positions at sea or in port. To identify the positions corresponding to fishing trips, and to resample the trajectories into elementary straight moves (Turchin, 1998), we used the set of 3 pre-processing algorithms described in Bertrand et al. (2005, 2007). From the raw positions, we identified 15,975 fishing trips operated by 563 vessels. VMS data held in the database comprises of vessel ID, date, hour, longitude and latitude. From these raw data we derived higher order variables for each elementary straight move: speed (ratio of move length to move duration), speed variation (difference between the speeds of two consecutive moves), and change of direction (absolute angle between the headings of two consecutive moves). Of the raw and derived variables, five were selected as important from the viewpoint of the fishing operation: speed, hour, absolute change of direction, and two calculations of speed variation (current and next position, and current and previous position). All the other available variables that could be deduced from raw latitude–longitude data (distance, heading, etc.) were not included in the set of characterizing variables as they were not found to improve model performance. After pre-processing these variables (standardizing and linearization of the circular variables), they served as inputs to a neural network model.

In order to train the neural network, we needed a reference sample of fishing trips for which we knew where the fishing operations truly occurred. We used information collected by the at-sea observer program run by IMARPE since 1996 and which has sampled an average of 25 vessels almost continuously since that time. The observers collect among other information the exact position of the fishing operations and the corresponding catches. We selected from this data the fishing trips corresponding to the period and area of interest (142 fishing trips, 494 fishing operations). We then extracted the corresponding fishing trips from the VMS database. To build a training dataset, each vessel elementary move generated from the VMS data was assigned the five selected input

variables (speed, hour, absolute change of direction, and speed variation $\times 2$) and a Boolean variable where 1 identified a fishing operation and 0 was assigned to all remaining elementary moves. The remaining VMS elementary moves (the forecast dataset) corresponded to fishing trips where there were no corresponding at-sea observer records.

2.2. Design of the neural network

Neural networks have become a popular tool for classification. The type of neural network used in this study is a multilayer perceptron (MLP), which is probably the most widely used architecture for practical applications. They are supervised networks, so they require a desired output to be trained. They learn how to transform input data into a desired output response, so they are widely used for pattern classification. MLPs have been shown to be able to approximate any continuous function when a sufficient number of hidden nodes are used (Cybenko, 1989; Funahashi, 1989; Hornik et al., 1989). These properties make neural networks good tools for non-parametric classification as they do not assume any parametric form for distinguishing between categories. The MLP used in this study is made up of three neural layers: the input layer, the output layer, and a middle ‘hidden’ layer. The input layer consisted of the five input neurons, i.e. the speed and hour of the move, the absolute change of heading between the current and the previous move ($|\Delta\theta|$), the speed variation between the current and the previous move (Δv_{-1}) and the speed variation between the current and the next move (Δv_{+1}). The output layer (neuron) consisted of a simple two-class classifier: fishing set or no fishing set.

Fig. 2 displays the topology of a 5-3-1 MLP. In this network topology, the input layer is determined by the input signals. This upper layer sends these signals to neurons in the hidden layer. Each hidden neuron computes the weighted sum of the inputs, i.e. the inner product between its inputs and corresponding weights plus a ‘bias’ term. This quantity is then transformed using

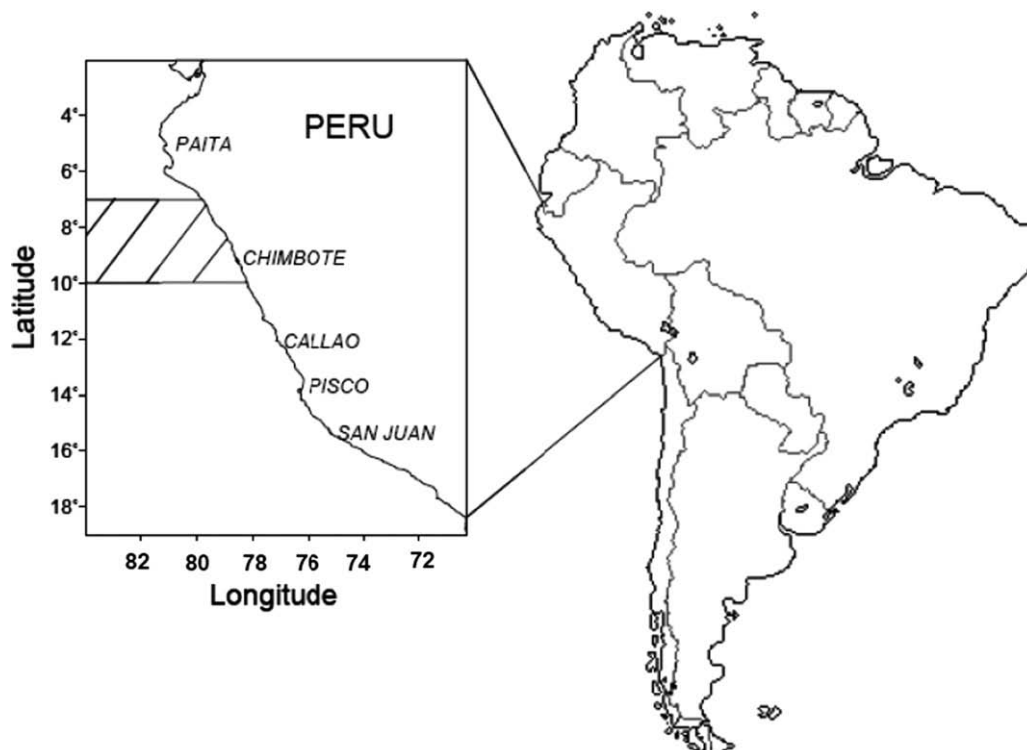


Fig. 1. Map highlighting the region of interest (7°–10° S off Peru).

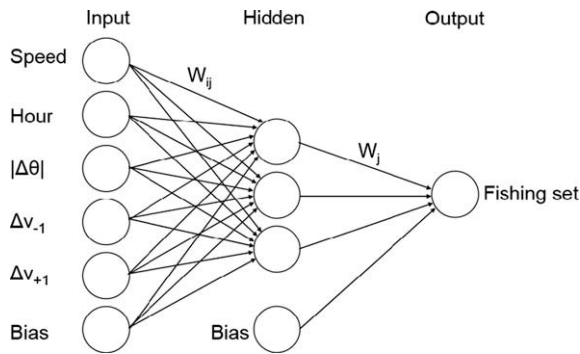


Fig. 2. Topology (5-3-1) of the multilayer perceptron (MLP), a kind of supervised artificial neural network, used to identify fishing sets from VMS data.

an activation function. The output layer processes its signal in the same manner. Therefore, the neural network has multiple inputs (x_i , $i = 1, \dots, l$) which are non-linearly mapped to m intermediate variables called hidden neurons (h_j , $j = 1, \dots, m$), and which are then mapped to an output variable y . Mathematically, the relationship linking input to output can be described as follows:

$$h_j = \phi_1 \left(\sum_{i=1}^l w_{ij} x_i + b_j \right), \quad j = 1, \dots, m \quad (1)$$

$$y = \phi_2 \left(\sum_{j=1}^m \tilde{w}_j h_j + \tilde{b} \right) \quad (2)$$

The characteristics of this empirical model are determined by $m^*(l+1)$ weight parameters (w_{ij} and w_j) and $(m+1)$ bias parameter (b_j and b). For a two-classes classifier, one output neuron is sufficient. ϕ_1 and ϕ_2 are activation functions for the hidden and output layer. They can be any monotonic smooth function. A multiple linear regression is therefore a special type of neural network with no hidden layer and where ϕ_i are linear functions. By allowing ϕ_i to be monotonic non-linear functions the neural network can model the non-linear relationship that might exist between the input and output signals. In a neural network model, the weights between neurons are the connections between the problem and its solution. The weights and biases contain all the information about the network. Therefore, the objective is to train the network to obtain a combination of weights and biases that minimizes the error between the neural network output signal and the observed output. The most commonly used criterion is to minimize the least mean squares error function (MSE) between the simulated output (y) and the observed output.

To train the network, we used a back-propagation procedure (Reed et al., 1999). This procedure aims at adjusting the weights and biases of the network to minimize the error function. Back-propagation adjusts the weights in the steepest descent direction in which the performance function is decreasing most rapidly. We used the Levenberg–Marquardt algorithm that has the major advantage of speed.

One of the problems that occur during neural network training is called overfitting. The error on the training set is driven to a very small value, but when new data is presented to the network the error is large. The network has memorized the training examples, but not learned to generalize to new situations. We use an efficient technique for improving the generalization performance of the MLP, called early stopping. In this technique the data is divided into three subsets. The first subset is the training set which is used to compute the gradient and update the weights and biases of the network. The second subset, the validation set, is used to stop the training when the error on the validation set begins to rise (i.e. the

network begins to over-fit the training data) and the weights and biases at the minimum of the validation error are returned. The test set error is not used during the training, but it is used to compare different models. Another method for improving generalization, called Bayesian regulation (MacKay, 1992) has also been tested but did not give better results than early stopping.

For achieving the balance between data-fitting and model complexity from the proposed performance function, we also aimed to find the best number of hidden nodes. Several statistical criteria were analyzed in order to find the best MLP architecture and generalization performance: (i) mean squared error (MSE), (ii) correlation coefficient (r) and (iii) the correct and incorrect predicted classification rate of fishing operations with respect to the observed fishing operations. The output of the MLP is a real number with range in $[0, 1]$. We therefore needed to select a threshold on the output to provide the percentage of detections correctly and incorrectly classified. This threshold was chosen so that the total number of identified fishing sets was about the same as the number of observed fishing sets. Its value was set at 0.5.

For each model architecture tested, sensitivity analyses were performed by way of multiple test runs starting from random initial weights to decrease the chance of getting trapped in a local minimum and to find stable results. To compare the results obtained with the MLP, we also used a generalized linear regression model directly adapted using the MLP topology. We used a MLP with one input layer, one output logistic layer and no hidden layer, which is equivalent to a generalized linear regression model with logistic function. The same threshold (0.5) was used to compute the classification.

2.3. Training of the neural network

We trained the MLP described in the previous section with different number of neurons in the hidden layer to find the best architecture to predict fishing operations. The MLP with one hidden layer was tested using hyperbolic tangent sigmoid and logistic sigmoid activation functions for hidden (ϕ_1) and output layers (ϕ_2), respectively. Other activation functions were also used but did not perform as well. The MLP with two hidden layers was also tested but no significant improvement was observed. Training was confined to 2000 iterations, but in most cases there were no significant improvement in the MSE after 300 iterations. The MLP was tested with the number of hidden nodes ranging from 1 to 10, while the training set size was set up randomly as 75% of the sample set. The validation and testing sets each took half of the rest. For reliable results and to better approximate the generalization performance for prediction, each experiment was repeated 50 times with different initial weights, training, validation and testing sets. The reported values were averaged over the 50 independent runs.

2.4. Comparing fish stock and fishing operations distributions

We tested the hypothesis that the distribution of fishing operations was correlated to the distribution of the anchovy stock using two approaches. The first relied on a visual comparison of monthly maps of spatial distribution of fishing sets identified by the neural network with the concomitant spatial distribution of acoustic biomass as observed by 10 IMARPE acoustic surveys (exact dates of these surveys are given in Table 1). The second test was based on a comparison of three spatial indices describing general features of the concomitant distributions of fishing sets and anchovy stock. Acoustic data were collected with a scientific echosounder system (38 and 120 kHz split-beam SIMRAD EK500, Kongsberg SIMRAD AS, Norway), calibrated using standard procedures (Foote et al., 1987). The water column was sampled to depths of 250 and

500 m, for 120 and 38 kHz, respectively. The survey design consisted of parallel transects running from 3.7 km from the coast to approximately 185 km offshore, with inter-transect distances varying between 26 and 30 km. Acoustic backscattered energy by surface unit (s_A) was recorded in each elementary sampling distance unit (ESDU) of 1852 m (1 nautical mile). Species composition was determined from the combination of information from trawling, echo-trace characteristics, and abiotic conditions. Data corresponding to anchovy for the study area were selected, with s_A used as an index of anchovy abundance.

For the comparison of spatial distributions of fishing sets and anchovy abundance (given by non-zero s_A ESDU) we first computed an index of the longitudinal extent covered by each dataset, using mean distance to the coast as a proxy for longitudinal extent. For Peruvian anchovy, longitudinal extent can be used as an indicator of adverse warm conditions (i.e., anchovy highly vulnerable to the fleet) or cold favourable conditions (Mathisen, 1989). A classical illustration for anchovy population relies on the effect of El Niño events on its spatial patterns. Typically, the stock distribution follows the inshore contraction of cold coastal waters (Valdivia 1978; Bertrand et al., 2004), which increases its availability to fishermen, resulting in magnification of catchability when the stock is, at the same time, particularly vulnerable to unfavourable environmental conditions. For fishing sets, the average distance to the coast was estimated with an accuracy of 10 nm (18.5 km) (isoparalitoral areas, IMARPE unpublished data) and then averaged by month. The mean distance to the coast (MDC) for anchovy distribution was estimated as the average distance to the coast of the ESDU associated with anchovy presence. Because fish acoustic data usually include a high proportion of ESDU values with a very low s_A , we weighted the distance estimates by the corresponding ESDU s_A value.

For the second index we estimated the area covered for each distribution (fishing sets and fish abundance). We first determined the minimum convex polygon encompassing all points of the distribution (for an example see Fig. 7), and then estimated the area of these polygons using an algorithm based on a partition of the polygon into a series of elementary triangles.

The third index characterized the patchiness or clustering of the spatial distributions using Ripley's K function (Ripley, 1976). Designed for analysing spatial point processes, the K function is based on the estimation of the average number of events occurring in a disc of radius t

$$\hat{K}(t) = \frac{A}{n^2} \sum_i \sum_{j \neq i} I(d_{ij} \leq t) \quad (3)$$

where $I = 1$ for each point within t distance otherwise $I = 0$, A is an estimate of the area covered by the process, d_{ij} the distance between the i th and the j th point, and n the total number of points of the process. This estimator is biased for large values of t as edge effects may lead to an underestimation of the number of neighbours for the points located at the edges of the process. Several correction factors may be applied (e.g. Dixon, 2002), but one empirical way to limit the impact of these edge effect is to consider only t values smaller than half of the main dimension of the domain. Here we used $t < 18.5$ km as this represented the smallest mean distance to the coast for both anchovy and fishing set distributions. To quantify the degree of clustering of the observed distributions, we calculated the area comprised (the sum of the differences) between the K function estimated from observed data with a random reference K function. The observed distribution of fishing sets is a point process which can be directly compared to a theoretical complete random distribution (homogeneous Poisson process), for which we have

$$K(t) = \pi t^2 \quad (4)$$

For anchovy distribution, we had to adapt this approach in two ways. First, anchovy distribution is essentially a 2D field distribution sampled by a 1D continuous transect. From this data, we defined as a point process the occurrence of ESDU presenting s_A values above $500 \text{ m}^2 \text{ nm}^{-2}$. This threshold was numerically defined as the median value for the mean non-zero s_A by survey. Empirically, this threshold can be considered to represent fish densities of primary interest to the commercial fleet. Second, because the survey is systematic, the locations where the process may occur are fixed. The random hypothesis as defined here is therefore not a true random spatial process but a random distribution of the selected ESDUs (s_A above $500 \text{ m}^2 \text{ nm}^{-2}$) among all the existing ESDU locations. For each survey, we generated 100 replicate random distributions of high density ESDUs among transects of the same survey. We defined the clustering index as the area comprised (the sum of the differences) between the experimental K function and the higher K function from the random replicates. Values of K are expressed in nm^2 . The clustering index, defined as a difference between two K functions, was therefore also expressed in nm^2 .

To explore the potential relationships between fish and fishing sets distributions, we estimated the correlation for these indexes between each survey period and the closest month of fishing activity (see Table 1 for time references). For the tests we calculated Pearson's correlation statistic for normally distributed variables (total area of distribution) and Spearman's non-parametric rank correlation for non-normally distributed variables (mean distance to the coast and the clustering index).

3. Results

3.1. Identification of fishing operations

The performance of a neural network depends on the number of neurons in the hidden layer. Generally speaking, the more neurons there are in the hidden layer, the better the network performs dur-

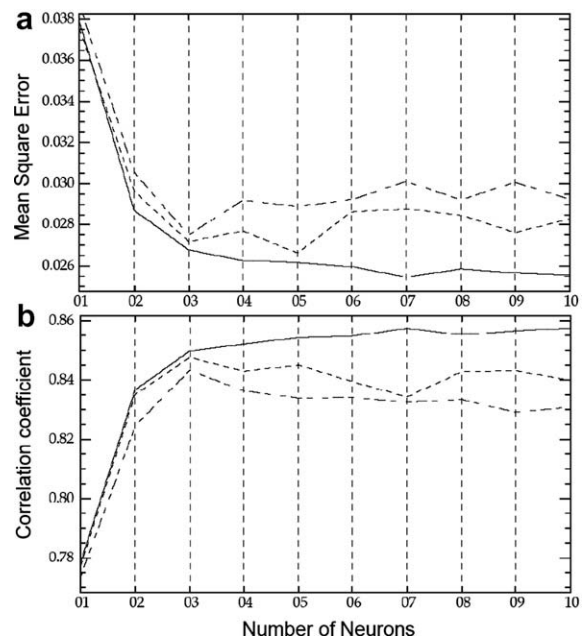


Fig. 3. Performance of the MLP according to the number of neurons in the hidden layer: (a) mean square error (MSE) and (b) correlation coefficient (CC) between observed and predicted fishing sets for the training (solid line), validation (dashed line) and test (dashed-dotted line) dataset. MSE and CC were estimated as an average of 50 independent runs. From this figure, the best MLP used for prediction is chosen to be the one with 3 neurons in the hidden layer.

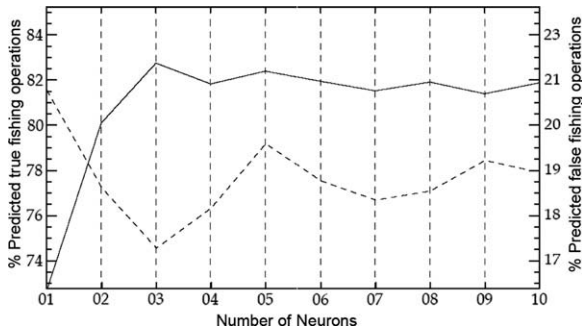


Fig. 4. Correct and incorrect classification rates averaged over 50 independent runs, given different numbers of hidden nodes. The percentage shown represents the number of correctly and incorrectly identified fishing operations divided by the number of real fishing operations. The results were consistent with Fig. 3. MLP with three neurons gave about 83% of correct classification (solid line) and 17% incorrect ones (dashed line) which is a good generalization performance for predicting fishing operations.

ing training. However, the more neurons there are, the higher is the risk of over-fitting, which leads to poorer predictions. This is illustrated by Fig. 3 which gives the average of the MSE (Fig. 3a) and correlation coefficient (Fig. 3b) of 50 runs, given different numbers of hidden neurons for the training, the validation and the test dataset.

While the correlation coefficient monotonically increases with the number of neurons for the training set, it reaches a maximum for both the validation and test set at about three neurons. With more neurons in the hidden layer, this value decreases significantly, indicating that there is over-fitting with more than three neurons. Similar results are obtained with the MSE, with the smallest MSE for the testing set obtained with three neurons. The best MLP network from structural learning is therefore chosen to be three nodes in the hidden layer. Fig. 4 gives the average of the correct and incorrect classification rates of 50 runs, given different numbers of hidden nodes. The results were consistent with

Fig. 3. MLP with three neurons gave about 83% of correct classification and 17% incorrect ones which is a good performance for predicting fishing operations. Regardless of the number of neurons considered in the hidden layer, the performance of the MLP exceeded that of the generalized linear regression model (65% correct classification, 16% incorrect classification). Similarly, the speed threshold (Fig. 5) overestimated by 182% the number of observed fishing sets, justifying the use of a more complex tool. The neural network was therefore used to forecast fishing operations for those trips where no observers were onboard. The neural network identified between 129 and 4088 fishing set positions (mean 1744) for the 22 study months and 3 degrees latitude study area (Table 1). Variability in the number of sets per month is largely caused by the imposition of short term access restrictions.

3.2. Spatial distribution of fishing sets and comparison with acoustic biomass

Fig. 6 graphically compares the spatial distribution of fishing sets with concomitant acoustic biomass. In general the patterns are broadly similar. Fishing sets were located near to the shore when high acoustic densities were concentrated along the coast (e.g. October 2000, November 2000 and October 2001), and conversely during times when higher levels of anchovy abundance were recorded offshore (e.g. July 2000). Large clusters of high density fish aggregations are highly coincident with the distribution of fishing sets (e.g. March 2000, April 2001). The degree of spatial coincidence is less apparent as the patch size of fish abundance decreases. At times catches are not seen to occur in areas where anchovy densities appear to be very high (see the small offshore patch of fishing sets in November 2000); conversely some high density but small anchovy patches are not tracked by fishing set distribution (see the offshore anchovy patch in October 2001).

For the distribution of fishing sets, mean distance to the coast varied between 18.5 km (November 2001) and 90.9 km (July 2002). The total area covered by these fishing sets (See Fig. 7a and b for an example of convex polygon used) ranged between

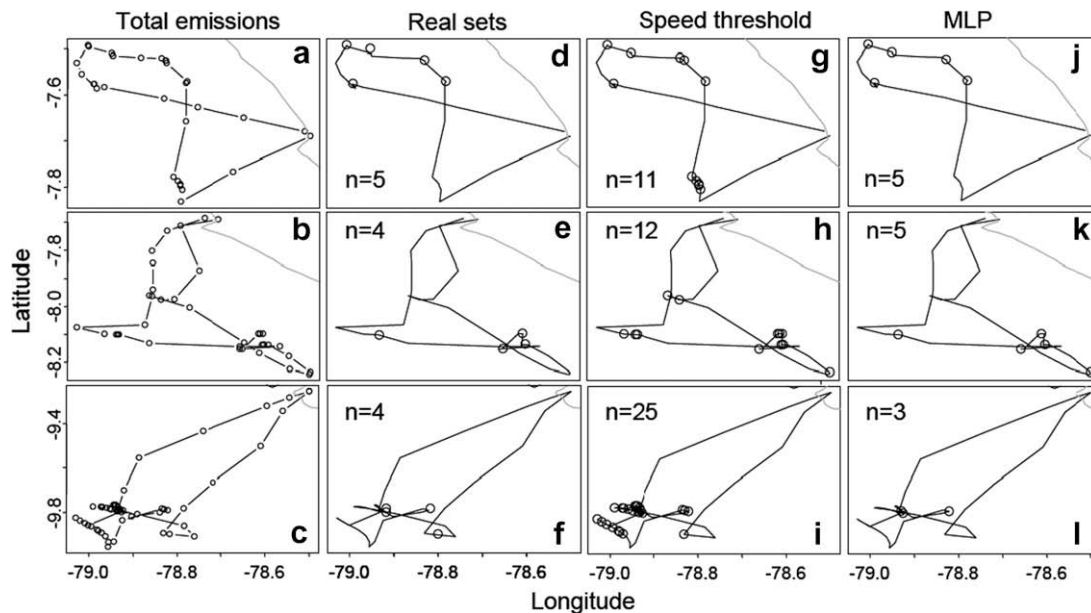


Fig. 5. Tracks of three fishing trips (horizontal succession of pictures) showing the total emissions during the trip (Fig. 5a–c), the number (n) and position of real fishing sets registered by observers on board (Fig. 5d–f), the number (n) and position of the sets estimated only by speed threshold (Fig. 5g–i) and the number (n) and position of the sets estimated by the MLP (Fig. 5j–l). Note that in the first trip the MLP optimized the identification process by successfully finding the real sets, in the second trip the MLP overestimated by one the number of real sets and during the third one the MLP underestimated by one the real sets. Although the last two cases show examples of misclassification, MLP is statistically significantly more powerful than other methods tested for identifying fishing set locations.

5631 km² (November 2001) and 56,714 km² (July 2000). The clustering index (see Fig. 7c and d for an example of estimated Ripley *K* function) varied between 26,836 km² (June 2001) and 279,410 km² (October 2000).

There was sufficient data from the acoustic survey to allow a comparison of the indices computed for anchovy distribution for 10 corresponding months (Table 1). The number of ESDU

(1.852 km long) with presence of anchovy ($s_A > 0$) varied between 551 and 1451. The corresponding mean distance to the coast varied between 18.9 km (October 2001) and 91.9 km (July 2000). The total area of the polygon enclosing ESDU having anchovy presence varied between 37,105 km² (April 2002) and 82,664 km² (July 2000). Finally the clustering index was maximum in July 2000 (175,378 km²) and minimum in April 2002

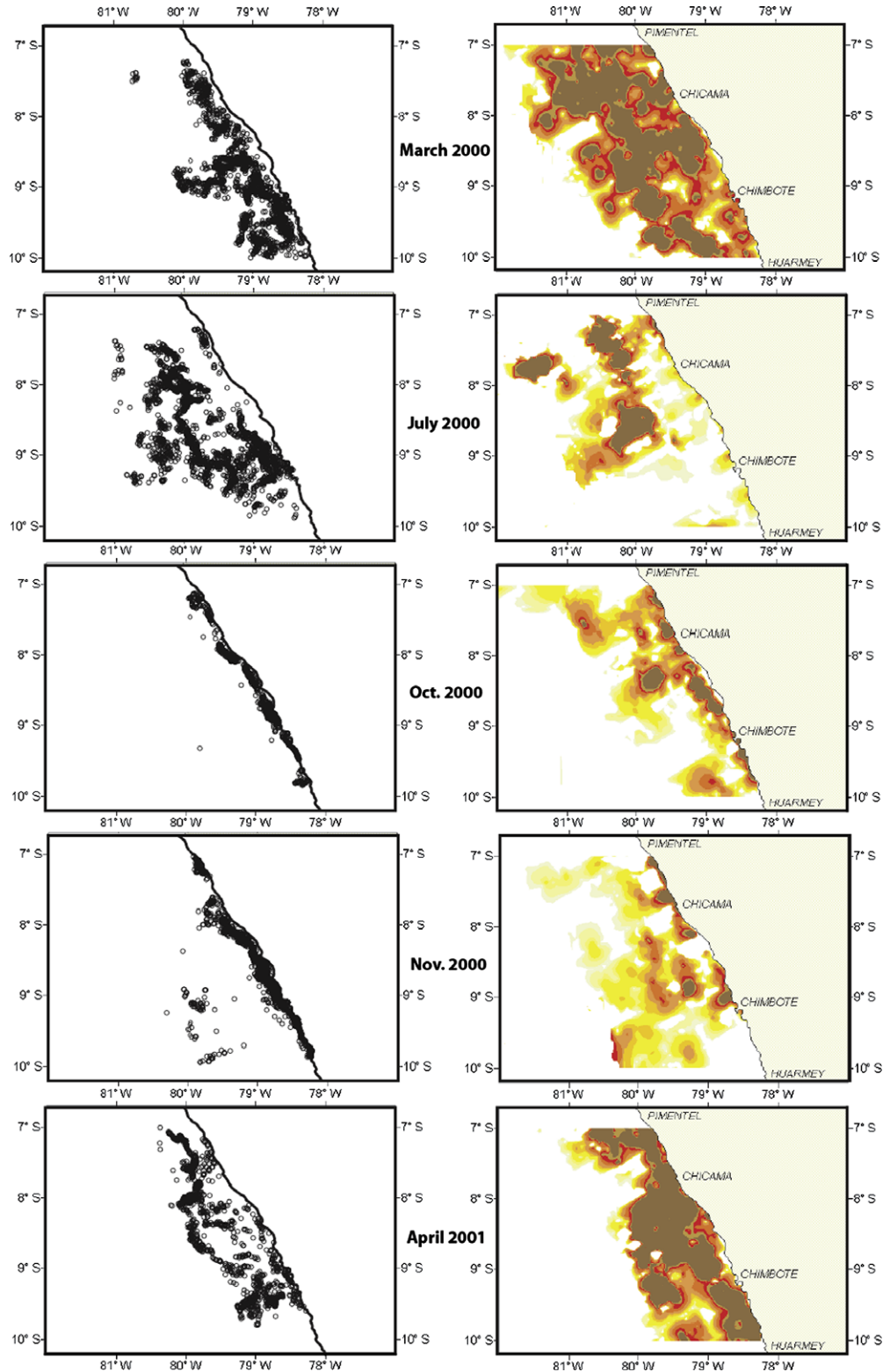


Fig. 6. Monthly maps of spatial distribution of fishing sets identified by the MLP and the corresponding spatial distribution of acoustic biomass as observed by 10 IMARPE scientific survey performed during the periods of interest (exact dates of these surveys are given in Table 1).

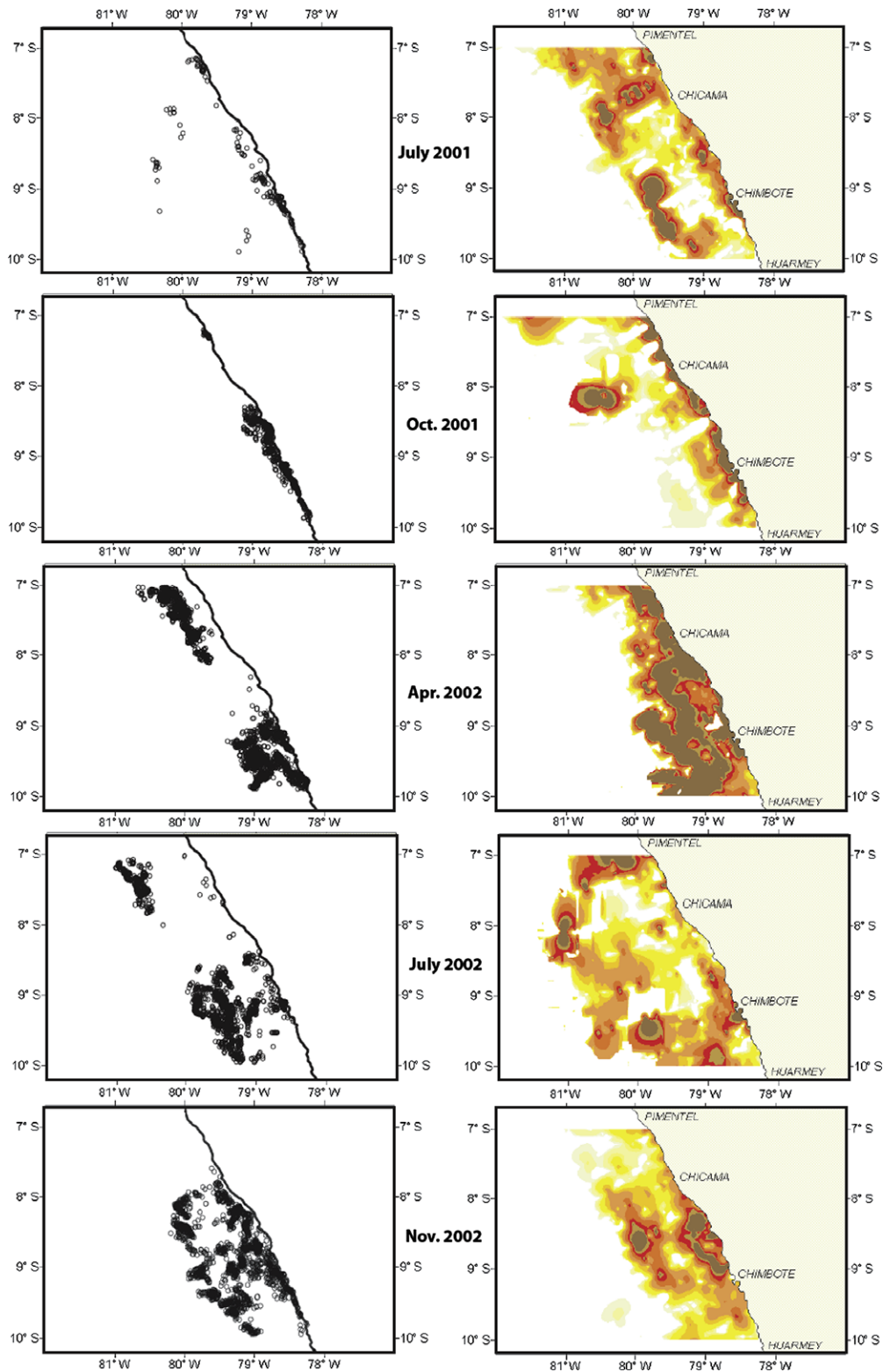


Fig. 6 (continued)

(36,858 km²). Correlations between corresponding indices from anchovy and fishing set distributions were significant ($p < 0.05$) for the mean distance to the coast and for the clustering index (Table 2). The correlation between the area of the polygons enclosing fish and fishing set distributions was not found to be significant.

4. Discussion

4.1. On the neural network

In this study we showed the effectiveness of neural networks for identifying the location of fishing operations. The use of a mul-

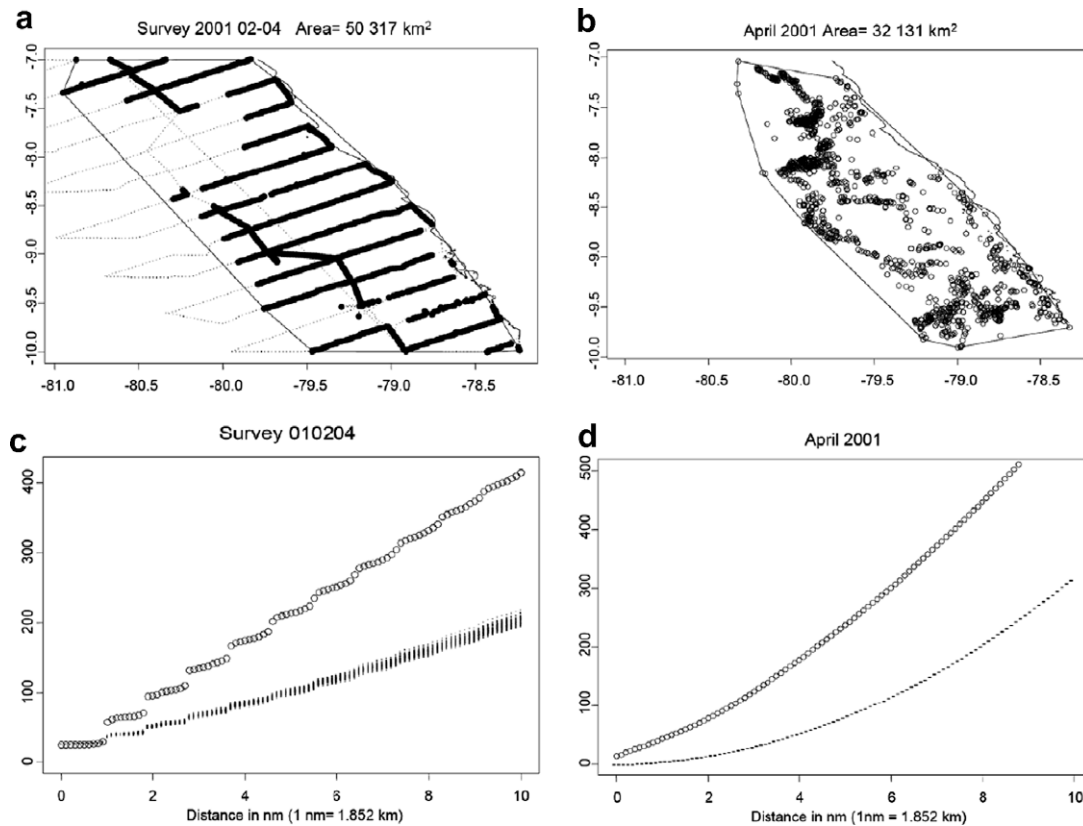


Fig. 7. Example of the minimum convex polygon used to determine the area encompassed by (a) the anchovy distribution and (b) the fishing sets distribution for the month April 2001. Below are represented the corresponding K function estimations for fish (c) and for fishing sets (d). In (c), dots represent the empirical K function; below are represented the 100 K functions corresponding to the 100 replicates of simulated random distributions. In (d), the dotted line represents the empirical K function and the dashed line represents the K function for a theoretical complete random (Poisson) spatial distribution. The clustering index was estimated as the area comprised between the empirical K and the simulated/theoretical random distribution K .

Table 2

Correlation results between fishing and fish indicators, n number of individual, ρ Pearson or Spearman correlation coefficient, p -value probability of type I error.

Descriptor	n	ρ	p value
Mean distance to the coast	10	0.78 (Spearman)	0.0200
Total area of distribution	10	0.61 (Pearson)	0.0587
Clustering index	10	0.77 (Spearman)	0.0220

tilayer perceptron allowed us to properly identify 83% of the fishing operations, significantly outperforming linear methods. The ability of neural networks to capture non-linear patterns among a collection of inputs allows them to be robust classifiers for complex systems. The performance values verify that this particular neural network has potential to identify fishing operations. Improvements, however, could still be made. Other types of neural networks, such as Kohonen Maps, as well as different classification techniques, such as support vector machine, could be tested to see whether identification performance can be further improved.

4.2. Fishing activity as an indicator of the fish stock condition

There was generally a high level of visual agreement between the spatial distributions of anchovy and fishing sets. The few discrepancies noted may have several explanations: (1) a slight time lag between acoustic and fishery data (this is the case for October 2001 which was compared to acoustic data collected in September); (2) only few days in a month open to fishing, as in July 2001, where there are too few fishing sets to reliably track anchovy

distribution; (3) when anchovy is dramatically abundant, fishers may tend to preferentially exploit the more coastal aggregations (see March 2000 for instance); and (4) the port location may also influence fishing sets distribution, with areas closer to port being preferentially exploited. However, in the Peruvian anchovy fishery, fishing power is so strong (in terms of fleet size: around 1700 vessels for the industrial sector; in terms of number and latitudinal extent of the landing points, spanning all the Peruvian littoral), and anchovy distribution is so narrow in longitude (less than 200 nm), that the effects of these biases are minor and do not affect the overall ability of fishing operations to effectively track the main pattern of anchovy stock distribution.

The distributions of anchovy abundance and fishing sets tend to exhibit a seasonal pattern. Highest values for the mean distance to the coast and the total area of the polygon of presence are found during the austral winter (July). During this time the coastal upwelling is stronger and cold coastal upwelled waters (CCW), the habitat for anchovy, cover a wider extent (Mathisen, 1989; Muck et al., 1989; Bertrand et al., 2004). The reverse situation occurs in austral summer. Despite the clear seasonal patterns in environmental conditions, similar patterns are not apparent for the clustering indexes. Spatial clustering of the anchovy stock is thought to be more dependant on meso-scale physical features, such as eddies (Hyrenbach et al., 2006; Bertrand et al., 2008) which dynamic is influenced by non-periodic oceanic events, such as the arrival of oceanic Kelvin waves in the coastal system (Lengaigne, 2004).

We found significant correlations between fish and fishing set distributions for the mean distance to the coast and for the cluster-

ing index. Thus despite the potential biases that may affect the ability of fishing operations to track anchovy distribution (see above), and some spatial discrepancies for small patches of fish abundance, we can assert that the distribution of fishing sets do indeed capture the main features of anchovy stock distribution, such as longitudinal extent and patchiness. Of the three spatial indices, the correlation between the areas covered by anchovy and fishing sets failed to be significant. One explanation could be that surface estimation was more sensitive to the high number of low s_A ESDUs, abundance values that fishers do not consider to be commercially exploitable. It will be interesting in the future to extend the time series to examine in more detail the relationships described by the relatively small sample size available for this study (10 periods could be compared).

Both of the spatial dimensions, longitudinal extent and clustering, are closely related to fish catchability and vulnerability. High clustering and low distance to the coast correspond to situations where fish biomass is concentrated in a small area, and thus make fish aggregations easier to detect, and to catch (e.g. Valdivia, 1978; Csirke, 1989; Fréon and Misund, 1999). In other words, the stock is more vulnerable to the fishing fleet in these situations. Consequently, times when the fleet is found to be highly concentrated in the coastal zone (e.g. October 2001 in Fig. 6), or highly clustered, should be used as a warning signal of anchovy being highly vulnerable to the fishery, and lead to management measures aimed at reducing fishing effort.

4.3. Perspective opened by the use of spatially explicit fishing data

Because fishing activity constitutes, albeit indirectly, the main sampling effort on exploited populations, catch per unit effort (CPUE) has long been and is still widely used as an indicator of stock size by fishery management authorities. The use of CPUE may, however, be questionable with anchovy, because of the strong variability in catchability (e.g. Csirke, 1989). A number of studies have shown that an important part of this variability is explained by the spatial dynamics of fish populations and the fleets that exploit them (e.g. Winters and Wheeler 1985; Csirke, 1989; Crecco and Overholtz 1990; Rose and Leggett, 1991; Hilborn and Walters, 1992; Swain and Sinclair 1994; Petitgas 1998; Gaertner and Dreyfus-Leon 2004). Hilborn and Walters (1992) notes that “spatial mapping of CPUE should be done whenever possible to determine...how the spatial distribution of the stock and effort are changing”. Our study has shown that with the advent of VMS technology we are now able to produce routine, near real-time and comprehensive maps (whole fleet) of the distribution of fishing effort. We noted above how information on the location of fishing sets provides useful insights into the condition of the Peruvian anchovy stock and its vulnerability to fishing, and in turn can be used to inform management measures aimed at reducing fishing pressure in an adaptive manner. An important next step will be to combine information on fishing set locations with catch statistics for each trip in order to develop a more complete understanding of the spatial distribution of the catches made by the Peruvian anchovy fishery.

The availability of spatially explicit catch statistics has considerable value in fisheries science, in part to address issues of catchability mentioned above, but also to improve our understanding of fishers' behaviour and to forecast the spatial allocation of effort. These last questions, which constitute an important field of fisheries science, have been addressed mainly through limited observational studies (limited in space, in time and in number of individuals observed) or through numerical models. Allen and McGlade (1986), for instance, were interested in the strategies developed by fishers in searching for fish. They established through a simulation model the existence of two types of fishermen strat-

egies: the stochasts (or risk takers) and the Cartesian (or followers). Millischer and Gascuel (2006) studied, through an individual based model, the impacts of communication and cooperation between vessels during fish searching activities. Spatially explicit catch data will allow a return to the underlying assumptions of this kind of models, to validate or invalidate their general results, and hopefully shed light on the processes contributing to fishers' behaviour. This will be an important step forward as strategies for fishing effort allocation directly impact the effectiveness of fishery management measures. Management measures usually have a spatial component, whether explicit through marine protected areas, marine reserves, or temporary zone closure, or implicit through regional quotas (Babcock et al., 2005). A number of studies have emphasized the importance of testing the effect of different spatially explicit management devices on fisher's behaviour and to forecast their efficiency (e.g. Walters et al., 1999; Sanchirico and Wilen 2001; Smith and Wilen 2003; Hutton et al., 2004; Mahevas and Pelletier, 2004). Spatially explicit fishing data should prove particularly beneficial in this regard by ensuring that the assumptions of the forecasting simulation tools are more realistic and closely adapted to each fishery.

5. Conclusions

This work aimed to assess the extent to which the distribution of fishing operations could track the distribution of the Peruvian anchovy stock, and to assess how fisheries-dependent data could complement acoustic estimates of fish abundance from scientific surveys in an adaptive management process. Fishing set positions were routinely available for only a very small fraction of the fleet (1.5%). We therefore developed an automatic process for the identification of fishing set positions for the entire fishery from vessel trajectories as routinely collected in real-time by VMS. A neural network approach provided the best results, being able to identify 83% of total fishing set locations. Two of the three spatial indices we tested (longitudinal extent and patchiness) found that the distribution of fishing sets and fish abundance were significantly correlated and showed that fishing activity reflects the main features of the spatial dynamics of the stock. These patterns can subsequently be used to inform levels of stock vulnerability. Our results further encourage the use of VMS data as a near real-time monitoring tool for the condition of the Peruvian anchovy stock. The framework is currently being integrated into daily monitoring and management.

Acknowledgments

The authors would like to thank Jaime Atiquipa and Mariano Gutierrez from IMARPE for their valuable aid in providing VMS and acoustic data, respectively, and Arnaud Bertrand from IRD for earliest discussions at the origin of the paper. We are very grateful to Sylvie Thiria, Carlos Mejia and Julie Leloup for fruitful discussions on neural networks. We warmly thank Paul Eastwood for his remarkable editing work and valuable comments on the manuscript. This work is a contribution of the UR 097 'ECO-UP' and the UMR 'LOCEAN' from IRD. This work was supported in part by the US National Science Foundation in Grant No. NSF0526392 to Sophie Bertrand.

References

- Allen, P.M., McGlade, J.M., 1986. Dynamics of discovery and exploitation: the case of the Scotian shelf groundfish fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 1187–1200.
- Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* 60, 201–222.

- Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. *Reviews in Fish Biology and Fisheries* 6, 221–242.
- Babcock, E.A., Pikitch, E.K., McAllister, M.K., Apostolaki, P., Santora, C., 2005. A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. *ICES Journal of Marine Science* 62, 469–476.
- Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2004. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and Fisheries* 5, 296–316.
- Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Diaz, E., Espinoza, P., Ledesma, J., Quesquén, R., Peraltilla, S., Chavez, F., 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: an analysis across multiple spatial scales. *Progress in Oceanography* 79, 264–277.
- Bertrand, S., Burgos, J., Gerlotto, F., Atiquipa, J., 2005. Lévy trajectories of Peruvian purse-seiners as an indicator of the spatial distribution of anchovy (*Engraulis ringens*). *ICES Journal of Marine Science* 62, 447–482.
- Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale invariant movements of fishermen: the same foraging strategy as natural predators. *Ecological Applications* 17 (2), 331–337.
- Bishop, C.M., 1995. *Neural Networks for Pattern Recognition*. Oxford University Press, Inc., New York, NY, 500p.
- Chen, D., Ware, D., 1999. A neural network model for forecasting fish stock recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 56, 2385–2396.
- Crecco, V., Overholtz, W.J., 1990. Causes of density-dependent catchability for Georges Bank Haddock *Melanogrammus aeglefinus*. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 385–394.
- Csirke, J., 1989. Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. ICLARM Conference Proceeding, pp. 207–219.
- Cybenko, G., 1989. Approximation by superpositions of a sigmoidal function. *Mathematics of Control, Signals and Systems* 2, 303–314.
- Davoren, G.K., Montevecchi, W.A., Anderson, J.T., 2002. Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murre. *Marine Ecology Progress Series* 245, 259–272.
- Deng, R., Dichmont, C., Milton, D., Haywood, M., Vance, D., Hall, N., Die, D., 2005. Can vessel monitoring system data also be used to study trawling intensity and population depletion? The example of Australia's northern prawn fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 62, 611–622.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S., 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science* 60, 371–380.
- Dixon, P.M., 2002. Ripley's K function. In: El-Shaarawi, A.H., Piegorisch, W.W. (Eds.), *Encyclopedia of Environmetrics*, vol. 3. John Wiley and Sons, Ltd., Chichester, pp. 1796–1803.
- Dreyfus-León, M., 1999. Individual-based modeling of fishermen search behaviour with neural networks and reinforcement learning. *Ecological Modelling* 120, 287–297.
- Fauchald, P., Erikstad, K.E., Skarsfjord, H., 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and preys. *Ecology* 81, 773–783.
- Fine, T.L., 1999. *Feedforward neural network methodology*. Springer-Verlag, New York, 356p.
- Foot, K.G., Knudsen, H.P., Vestnes, D.N., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of Acoustic Instruments for Fish Density Estimation: A Practical Guide. *ICES Cooperative Research Report*, No. 144, pp. 1–69.
- Fréon, P., Misund, O.A., 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Blackwell Science, 348p.
- Frontier, S., 1987. Applications of fractal theory to ecology. In: Legendre, P., Legendre, L. (Eds.), *Developments in Numerical Ecology*. Springer-Verlag, Berlin, pp. 335–378.
- Funahashi, K., 1989. On the approximate realization of continuous mappings by neural networks. *Neural Networks* 2, 183–192.
- Gaertner, D., Dreyfus-León, M., 2004. Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse seine fishery simulated with artificial neural networks. *ICES Journal of Marine Science* 61, 812–820.
- Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–1772.
- Hilborn, R., Walters, C.J., 1992. *Quantitative Fisheries Stock Assessment. Choice Dynamics and Uncertainty*. Chapman and Hall, New York, London, 570p.
- Hornik, K., Stinchcombe, M., White, H., 1989. Multilayer feedforward networks are universal approximators. *Neural Networks* 2, 359–366.
- Hutton, T., Mardle, S., Pascoe, S., Clark, R.A., 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Journal of Marine Science* 61, 1443–1452.
- Hyrenbach, K.D., Veit, R.R., Weimerskirch, H., AndHunt Jr., G.L., 2006. Seabird associations with mesoscale eddies: the subtropical Indian Ocean. *Marine Ecology Progress Series* 324, 271–279.
- Lengaigne, M., Boulanger, J.P., Delecluse, P., Menkes, C., Slingo, J., 2004. Westerly wind events and their influence on coupled ocean-atmosphere system: a review. *AGU Monograph: Earth Climate: The Ocean-Atmosphere Interaction*, pp. 49–71.
- MacKay, D.J.C., 1992. Bayesian interpolation. *Neural Computation* 4 (3), 415–447.
- Mahevas, S., Pelletier, D., 2004. ISIS, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling* 171, 65–84.
- Mathisen, O.A., 1989. Adaptation of the anchoveta (*Engraulis ringens*) to the Peruvian upwelling system. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. ICLARM Conference Proceeding, pp. 220–234.
- Maunder, M., Hinton, M., 2006. Estimating Relative Abundance from Catch and Effort Data, Using Neural Networks. *Inter-American Tropical Tuna Commission, Special Report*, 15, 18p.
- Millischer, L., Gascul, D., 2006. Information transfer, behavior of vessels and fishing efficiency: an individual-based simulation approach. *Aquatic Living Resources* 19, 1–13.
- Mills, C.M., Townsend, S.E., Jennings, S., Eastwood, P., Houghton, C.A., 2007. Estimating high resolution trawl fishing effort from satellite-based vessel monitoring system data. *ICES Journal of Marine Science* 64, 248–255.
- Muck, P., Pauly, D., 1987. Monthly anchoveta consumption of guano birds, 1953 to 1982. In: Pauly, D., Tsukayama, I. (Eds.), *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. ICLARM Studies and Reviews, vol. 15, pp. 219–233.
- Muck, P., Fuentes, H., 1987. Sea lion and fur seal predation on the Peruvian anchoveta, 1953 to 1982. In: Pauly, D., Tsukayama, I. (Eds.), *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. ICLARM Studies and Reviews, vol. 15, pp. 234–247.
- Muck, P., Zafra de Moreno, A., Aranda, C., 1989. The seasonal dynamics of sea surface temperature and its impact on anchoveta distribution off Peru. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. ICLARM Conference Proceeding, pp. 33–44.
- Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science* 62, 1150–1167.
- Pettigass, P., 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. *ICES Journal of Marine Science* 55, 443–453.
- Reed, R.D., Marks II, R.J., 1999. *Neural Smoothing: Supervised Learning in Feedforward Artificial Neural Networks*. The MIT Press, Cambridge, MA, 346p.
- Ripley, B.D., 1976. The second-order analysis of stationary point processes. *Journal of Applied Probability* 13, 255–266.
- Ripley, B.D., 1996. *Pattern Recognition and Neural Networks*. Cambridge University Press, 416p.
- Rose, G.A., Leggett, W.C., 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 48, 843–848.
- Russel, R.W., Hunt, G.L., Coyle, K.O., Cooney, R.T., 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. *Landscape Ecology* 7, 195–209.
- Sanchirico, J.N., Wilen, J.E., 2001. A bioeconomic model of marine reserve creation. *Journal of Environmental Economics and Management* 42, 257–276.
- Smith, M.D., Wilen, J.E., 2003. Economic impacts of marine reserves: the importance of spatial behavior. *Journal of Environmental Economics and Management* 46, 183–206.
- Swain, D.P., Sinclair, A.F., 1994. Fish distribution and catchability: what is the appropriate measure of distribution? *Canadian Journal of Fisheries and Aquatic Sciences* 51, 1046–1054.
- Turchin, P., 1998. *Quantitative analysis of movement. Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc., 396p.
- Valdivia, G.J.E., 1978. The anchoveta and el Niño. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 173, 196–202.
- Walters, C., Pauly, D., Christensen, V., 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539–554.
- Winters, G.H., Wheeler, J.P., 1985. Interactions between stock area, stock abundance and catchability coefficient. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 989–998.