Spatial patterns of the Argentine hake *Merluccius hubbsi* and oceanographic processes in a semi-enclosed Patagonian ecosystem.

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Running title: Spatial patterns of Argentine hake.

Abstract

Time-series of fishing position, landings, satellite-derived sea surface temperature and chlorophyll *a* concentrations were used to relate the spatial-temporal distribution of the Argentine hake *Merluccius hubbsi* with seasonal oceanographic processes in San Matías Gulf. Also, the seasonal effect of fishing on the hake population structure was analysed. During summer the fleet was concentrated over the area of the frontal system, obtaining the best catch-per-unit-effort (CPUE) of hake in relatively deep waters. In autumn, the dispersion of the fleet due to a reduction in CPUE coincided with the dissipation of the front, suggesting that the distribution and shoaling of the Argentine hake is associated with seasonal thermal structures. In spring, the thermal structure of the waters and the Chlorophyll *a* blooms seem to modulate the timing of spawning of hake, which occurs mainly in October-November. In addition, the fleet captured a higher proportion of females in the gonadal recovery stage during warm months (November to April). While winter catches (May to October) consisted mainly of males, the intense summer fishing may result in a high impact on the female population. This information is relevant to design of spatial management tools intended to provide biological sustainability to the hake fishery.

Keywords

Natural resources distribution, tidal front, trawl fishery, satellite-derived data, sustainable management.

Introduction

The physical properties of the oceans influence biological processes at all spatial and temporal scales (Mann 1992). Among the different physical variables that affect the distribution of marine organisms, the sea temperature is considered important, because many species are associated with thermal structures and specific thermal conditions (Perrota *et al.* 2001; Spinelli *et al.* 2012). Various species show high densities next to oceanic fronts (Reddy *et al.* 1995; Sabatini & Martos 2002), because these structures play a key role in ecological processes by allowing for an exceptionally high primary production, offering adequate feeding and/or reproductive habitats for nektonic species (fishes and squids) and acting as retention areas for larvae (Acha *et al.* 2004; Houde 2009; Spinelli *et al.* 2012). Similarly, areas with high chlorophyll-*a* (Chl *a*) concentrations, which indicate high phytoplankton biomass (Morel & André 1991; Huot *et al.* 2007) are related to limiting concentrations of nutrients (Aminot *et al.* 1998; Herut *et al.* 2007), show abundant fish and crustacean larvae (Wehrtmann 1994; Friedland *et al.* 1996) and high concentration of birds (Ballance *et al.* 1997) and marine mammals (Jaquet *et al.* 1996). In this respect, studying the areas with oceanic fronts and/or high Chl *a* concentrations may also be relevant to design measures for fisheries management and conservation.

On the Argentine Continental Shelf (ACS), frontal areas provide better foraging opportunities than non-frontal areas for a broad range of marine organisms (Alemany *et al.* 2009). Indeed, the oceanographic fronts are key marine structures in which to understand feeding and reproduction strategies, as well as migration patterns of local populations (Acha *et al.* 2004). Also, the thermal structure of the sea has been considered as an important variable in biological and fisheries studies, mainly in the prediction of recruitment, larval survival, spawning areas and catches as well as in the study of spatial and temporal changes in abundance of commercial species (Stuart *et al.* 2011).

Considering that the fact that changes in sea surface temperature (SST) could be used as an indicator of the structuring of water masses (i.e. thermal fronts) and also a relevant factor in the distribution and concentration of nutrients and phytoplankton (and consequently in the distribution and abundance of biological resources), integrated satellite-derived information of the SST and Chl *a* concentrations could be useful for analysing the relationships between distribution, abundance and catches of species of ecological and/or fisheries importance (Laurs *et al.* 1984). In pelagic fisheries, this approach has been widely used in scientific studies and commercial applications (e.g. Polovina *et al.* 2001; Platt *et al.* 2007; Saitoh *et al.* 2011; Druon *et al.* 2011). Moreover, fish species that integrate pelagic-demersal communities and develop most of their life cycles interacting with the intermediate and upper layers of the ocean, are good candidates for this type of study (Laurs *et al.* 1984). In the ACS, Wang *et al.* (2007) studied the influence of thermal features on the distribution of *Merluccius hubbsi* Marini, 1933 at the Patagonian shelf edge and found that hake have a positive association with thermal oceanic features.

Within San Matías Gulf (SMG, Patagonia, Argentina), many fishery species that play an important role in food webs (e.g. short-finned squid *Illex argentines* Castellanos, 1960) show dramatic interannual abundance variations for unclear reasons (Romero *et al.* 2007). Other species (e.g. *M. hubbsi*, the silver warehou *Seriolella porosa* Guichenot, 1848 and the Patagonian hoki *Macruronus magellanicus* Lönnberg, 1907) show seasonal variations apparently related to cyclical oceanographic processes (Ocampo Reinaldo 2010). Within this ecosystem, the fishing activity is performed mainly by industrial bottom trawlers and historically the most important fishery resource has been the Argentine hake (up to 80% of the annual landings) followed by the silver warehou in recent years (Romero *et al.*, 2010). The Argentine hake has demersal-pelagic habits, is an active predator that performs daily vertical migrations to feed in the upper layers of the water column (Angelescu & Prenski, 1987) and its behaviour and distribution seems to be strongly linked with the spatial structure of the pelagic system (Wang *et al.* 2007; Ocampo Reinaldo *et al.* 2011).

In this context, the seasonality of the catch-per-unit-effort (CPUE) of hake (Williams *et al.* 2010), together with the habits of the species and the strong oceanographic processes in SMG (Gagliardini & Rivas, 2004), suggest there might be a close relationship between the distribution of this species and the environmental cycles.

The aim of this study was to determine the relationship of the spatial-temporal distribution of *Merluccius hubbsi* with the oceanographic processes in SMG. Also, the seasonal effect of fishing on the hake population structure in relation to the formation of the frontal system was analysed. The results are discussed in relation to the spatial patterns and life cycle of the Argentine hake in SMG and the potential use of this information for the design of management measures for the fishery.

Methods

Study system: the environment and the fishery of Merluccius hubbsi.

San Matías Gulf (40°50´-42°15´S and 63°05'-65°10´W, Figure 1) is the second largest gulf in Argentina (about 20,000 km^2) and is a semi-enclosed basin with a maximum depth of 180 m in the central area (up to 55% of its total area is deeper than 100 m) and the mouth, at the eastern side, with a depth of 50-70 m (Chart H214 Argentine Service of Naval Hydrography; Williams *et al.* 2010). The northwest and southeast areas have different characteristics, separated by a seasonal tidal front (October to April;

Gagliardini and Rivas 2004). The northern area of the gulf shows higher temperature and salinity, with a strong thermocline, limited nitrate concentrations and a low turnover rate of its waters. The southern area shows lower temperature and salinity, a lack of stratification and a comparatively higher nitrate concentration (Rivas and Beier 1990). The observed SST of the northern and southern areas, when the tidal front is present, differs on average between 1 °C and 3 °C. During winter (May to September) the front vanishes and the differences are less than 1 °C (Piola and Scasso 1988; Gagliardini & Rivas 2004). The general circulation pattern in spring-summer is dominated by a cyclonic gyre, located at the northern half of the basin (70 km diameter approximately, Piola & Scasso 1998), which in combination with the frontal system determines the relative isolation of the northern water masses (Rivas & Beier 1990, Tonini 2010).

The Argentine hake is very common throughout the ACS at depths ranging from 50 to 500 m (Cousseau & Perrotta 2004) and the stock located at the SMG constitutes a unique independent demographic unit (Di Giácomo *et al.* 1993; Sardella & Timi 2004; González *et al.* 2007; Machado Schiaffino *et al.* 2011). The population structure of this stock seems to have been well preserved since the beginning of the fishery in 1971 (Romero *et al.* 2010; Ocampo Reinaldo 2010) compared with the ACS main stocks, which are considered overexploited (Figure 1, Aubone *et al.* 2004; Vaz-dos-Santos *et al.* 2010). In SMG, the Argentine hake spawns between August and March, with its maximum activity during October and November, indicating the most important reproductive schools are in the northern half of the basin (Di Giácomo *et al.* 1993; Ocampo Reinaldo 2010). This reproductive pattern led in 1998 to imposing a fishing ban on the industrial fleet in October and November (Figure 1, Ministerial decision 555/2003, Ministry of Economy of Río Negro Province, Argentina).

Environmental data

Environmental data from remote sensing were obtained and validated following the methods of Williams *et al.* (2010). Data from the Daily Level 1B local area coverage (LAC) of the Advanced Very High Resolution Radiometer (AVHRR) on-board the NOAA-N polar orbiting satellites and Sea-Viewing Wide Field of view Sensor (SeaWiFS) were acquired through the Argentine National Commission of Space Activities (CONAE). AVHRR data were obtained for the periods 2004–2007 and SeaWiFS data for the period 2004-2006 (SeaWiFS images were available only up to 22 December 2006).

Relatively cloud-free AVHRR and SeaWiFS scenes were processed applying the Multichannel Sea Surface Temperature (MCSST) (McClain *et al.* 1985) and OC4v4 algorithms (O'Reilly *et al.* 1998), respectively. AVHRR data were processed using Erdas Imagine and SeaWiFS data using SeaWiFS Data Analysis System (SeaDAS) version 5.2 (update#4) software (Baith *et al.* 2001). SST and Chl *a* were mapped to a WGS 84 reference system (datum WGS84, ellipsoid WGS84), on the cartographic Transverse Mercator projection (zone 4) at 1100 m of spatial resolution at nadir and co-registered with respect to a reference landmask. Land and cloudy pixels were flagged to zero and were not considered for the computations.

Monthly composites were created from the daily images, grouping all years and resulting in 12 scenes. The number of cloud-free pixels contributing to each monthly composite was spatially and temporally variable. The total numbers of cloud-free images used to create the scenes are shown in Table 1.

SST gradients (°C km^{-1}) were calculated from each monthly SST image by applying a Sobel operator in a 5x5 window size (Simpson 1990). The Sobel operator consist in two 5×5 convolution masks, which are used to calculate two images containing approximations for derivatives (in west-east and north-south directions) and assuming that there is an underlying continuous intensity function. At each pixel of the image, gradient magnitudes are computed and the results show how "abruptly" or "smoothly" the image changes at that pixel.

In order to evaluate the depths where the fleet operates, a topographic map of SMG was obtained by natural neighbour interpolation (250 m resolution, resampled to 1100 m) (Schneider 2009) based on the nautical chart H214 of the Argentine Service of Naval Hydrography.

Fishing activity data

The industrial bottom trawl fleet of SMG, which mainly target the Argentine hake, is characterized by relatively small vessels (20 to 36 m length and 400 to 800 HP), between 15 and 30 years old (Romero *et al.* 2007) that are fully capable of operating along the entire SMG for up to 8-10 days without returning to port. Most fishing captains are highly experienced local veterans. However, most of the catches are obtained following a process of "trial and error" and the success of a fishing haul generates repetitions within the same area. Conversely, a failed haul (i.e. a haul with a small catch) motivates the search of a different area. This leads us to assume that the fleet behaves as a relatively efficient predator and its persistence in an area is indicative of the location of the largest concentrations of resources (at least those commercially profitable). This approach allows us to infer the seasonal abundance of Argentine hake in different areas of SMG.

Data of the bottom trawl fleet activity for the 2004–2007 period were obtained from two different sources: 1) locations of hauls gathered by a Vessel Monitoring System (VMS, named SiMPO (González *et al.* 2004)) and, 2) monthly landings and fishing effort (to calculate the CPUE, in kg.h^{-1}) obtained from official logbook records of the Fishery Directorate of Río Negro province, Argentina (Millán 2007).

The SiMPO provided real-time data of vessel position, bearing and speed (every 96 minutes approximately) by on board Inmarsat D+ satellite transceivers. Criteria of speed were used to discriminate the SiMPO records that corresponded to fishing activities: records lower than 2.5 knots and higher than 4.0 knots were excluded, as they were not associated with fishing activity. All data were inspected to remove additional invalid records (e.g. speed at this range due to adverse weather conditions or port arrivals). The validity of the filtering criteria was evaluated by comparing on board observations of the duration of the hauls (Fisheries Observers Program of Río Negro Province -FOP-) with records transmitted over the same hauls by the SiMPO.

Fishing activity data were plotted as topographic representations using the same reference system of the environmental data. Data (counts of records per unit area) were grouped monthly and a spatial smoothing was performed to represent the areas with the highest fishing intensity. The smoothing was performed using a *Kernel density interpolation* (ESRI ArcGIS Desktop version 9.3), which involves placing a symmetrical surface over each point (records of fishing), evaluating the distance from the point to a reference location (one pixel on the SST image) based on a mathematical function, and summing the value of all the surfaces for the reference location. This procedure was repeated for every reference locations.

The mathematical function of surface density used was the normal distribution, according to:

$$CPUE_{sm} = g(x_j) = \sum\{ I_i * \frac{1}{1/(h^2 * 2\pi)} * e^{-(\frac{d_{ij}^2}{2 * h^2})} \} \qquad (1)$$

where $CPUE_{sm}$: smoothed $CPUE_{rec}$ that correspond to a particular pixel; *dij*: distance between the reference location and any point within the search radius considered; *h*: standard deviation of normal distribution (in this case the bandwidth or search radius); I_i: intensity of each point. In this case, a scale value of $I_i = CPUE_{rec}$ was used, being

$$I_i = CPUE_{rec} = (L_i / R_i) \qquad (2)$$

where $CPUE_{rec}$ is a new variable defined by landings (kg) per record of fishing; L_i: pooled total landings for each month for the entire 2004 – 2007 period; R_i: number of fishing records grouped for each month for the years 2004 to 2007. The bandwidth was 2500 m, and densities were calculated in a regular grid of 1100 m on the side of the square cell, consistent with the resolution of the satellite images used. Each monthly fishing activity map obtained was compared with the corresponding SST and Chl *a* monthly maps.

Also, topographic information obtained from the topographic map assign the bottom depth to each fishing position. The resulting depth distributions were compared using the Kolmogorov-Smirnov test for two independent samples, taking pairs of consecutive months ($\alpha = 0.05$).

Statistical analyses

The data used for the statistical analyses were obtained over a polygonal area from the mouth of the SMG to near its coastal line (9172 square pixels, 1100 m of spatial resolution, Fig. 1). The pixels with Chl *a*, SST, $CPUE_{sm}$ and SST gradients data were filtered and only pixels with data of all variables were used. The resulting pixels were split into two datasets: Autumn-Winter (May to October, absence of the thermal front) and spring-summer (November to April, with presence of the thermal front) (Williams *et al.* 2010). The variable Chl *a* had fewer pixels with data (due to a higher number of cloudy pixels), conditioning the selection up to 5167 pixels (56%) of total pixels available. Multivariate Partial Mantel tests were performed for each dataset in order to evaluate the general association between pairs of variables (Euclidean distance, 999 permutations, Bonferroni's corrected α=0.0084). Also, the $CPUE_{sm}$ and SST gradients for the original 9172 pixels were categorized as "High", "Medium" and "Low" (Table 2), and a Pearson χ^2 test was performed for each month. The hypotheses of independency were tested applying the Bonferroni's correction (α=0.042).

Additional biological and fishery information

Data from quasi-monthly samples were obtained on board by the FOP,from commercial catches (2004 to 2007). The monthly average sex ratio of *Merluccius hubbsi* catches was calculated on the basis of the data obtained from each haul. In order to evaluate the biological condition of the reproductive population of hake, gonadal stage and liver weight were recorded in mature females (larger than 27 cm, Ocampo Reinaldo, 2010). The hepatosomatic index (*HSI*) was calculated, as:

$$HSI = 100*(W_L/TW) \quad (3)$$

where W_L is the weight of the liver and TW is the total weight of the fish. Individual results were averaged to obtain an overall value of *HSI* for each month. Finally, monthly CPUE (kg.h^{-1}) of the *M. hubbsi*, *Seriolella porosa* and other species were grouped together and were analysed in order to describe the seasonal dynamics of the fishery.

Results

Considering the high temporal resolution (12 h) and availability of images from AVHRR sensors aboard NOAA satellites, 338 clouded-free images were obtained from January 2004 to December 2007. On the other hand, 130 SeaWiFS clear daily images were obtained from January 2004 to December 2006, because this sensor depends on the daylight and is aboard the OrbView-2 satellite, which has a temporal resolution of 24 h (Table 1). Monthly climatological SST and SST gradients maps confirm the presence of the frontal system during summer months (December to February) and its absence during winter (May to August). During September and October, the front begins to appear (increasing SST gradients), while in March and April it begins to disappear (Figs 2a, b). SeaWiFS images indicates that the Chl *a* distribution from December to February corresponds to the thermal front (Figure 2c): The warm waters of the north matched with minimal Chl *a* concentrations, while the cold waters of the south corresponded to higher Chl *a* concentrations.

The number of fishing records was in relation to the duration of the hauls and false negative records were seldom detected (Figure 3), whereas scarce false-positive records were totally discarded during *a priori* auditing.

The depth ranges of trawling remained largely between 80 and 160 m (Figure 4). With the exception of February-March and May-June, the distribution of the hauls in relation to the topography showed significant differences between consecutive months (Kolmogorov-Smirnov, α=0.05, Figure 4). During summer (December to March), the highest activity of the fleet was concentrated in the southeast and southern areas of the gulf, over (or near) the area of the thermal front (Figure 2d). The highest *Merluccius hubbsi* yields (700-900 kg.h^{-1}) were obtained during this season (Figure 5) and females outnumbered males in the catches (Figure 6).

During autumn-winter (April to September), yields of hake were lower (200-400 kg.h^{-1}) and males were dominant in the catches. The female hake captured by the fleet through the entire year showed rising gonadal maturation from January to September. In October and November, spawning occurred (Figure 7) as well as in December when an increase in post-spawning and gonadal recovery stages was observed. In agreement with the gonadal cycle, an increase in *HSI* was detected towards September, while from October it decreased to its lowest value in April (Figure 8).

Interestingly, from August to September, the fleet concentrated in the northern part of the Gulf (with no frontal areas, Figure 2d) and catches of the silver warehou *Seriolella porosa* rapidly increased, from almost null to a peak of 1000 kg.h^{-1} approximately. Catches of silver warehou rapidly decreased in September (Figure 5). During spring (October and November) the fleet moved southwards due to the implementation of the seasonal closure for the Argentine hake.

The remaining grouped species consisted mainly (up to 75-90%, in order of importance) of plownose chimaera *Callorhinchus callorynchus* (Linnaeus, 1758), mixed species, the flounders *Xystreurys rasile* (Jordan, 1891) and *Paralichthys spp*, the Patagonian hoki *Macruronus magellanicus* and the Parona leatherjacket *Parona signata* (Jenyns, 1841). The yields of this group did not show significant variations throughout the year, although in autumn-winter values were slightly higher.

The results of the Partial Mantel test showed that the variables Chl *a* and SST are associated throughout the year, as well as SST and SST gradients (Table 3). On the other hand, SST gradients were associated with Chl *a* in Spring-Summer and were not associated in Autumn-Winter. The $CPUE_{sm}$ was associated with SST and SST gradients only in spring-summer (Table 3).

The categorized SST gradients and $CPUE_{sm}$ were independent in May, June and July (Pearson χ^2 test, α=0.0042, Table 4), but the variables were dependent for the remaining months.

Discussion

This study contributes to the understanding of the spatial patterns of *Merluccius hubbsi* and its relations with the main oceanographic features of a semi-enclosed Patagonian ecosystem. A strong seasonal oceanographic pattern was confirmed, in accordance with the description by Gagliardini & Rivas (2004). According to Williams *et al.* (2010, 2012), SST data in this study area showed a good correlation between satellite-derived and *in situ* data . On the contrary, a poor correlation between *in situ* and remotely sensed Chl *a* concentrations has been found. Although in these results, the authors highlighted that the qualitative analysis revealed that AVHRR and SeaWiFS images reproduced temporal and spatial variability of SST and Chl *a* data measured *in situ* (Williams *et al*. 2010). Based on this information and the results of the SST and Chl *a* climatological maps, two areas with different environmental characteristics were confirmed in spring-summer: a warmer one in the northern area and a cooler one in the southern area. The spatial distribution of SST and Chl *a* was related to the position of this front in summer and the absence of the front in autumn-winter. These results are consistent with previous studies (Piola & Scasso 1988; Gagliardini & Rivas 2004; Williams *et al.* 2010), which reported two areas separated by a frontal system for most of the year. Satellite chlorophyll data jointly with SST, have been used in several studies to identify ecological regions in the ocean (e.g. Herut *et al.* 2000; Polovina *et al.* 2001;

More & Abbott 2002; Zainuddin *et al.* 2006). Generally, these ecological regions are not fixed in time or space and vary seasonally (Stuart *et al.* 2011). The results of this study showed a strong spatial association between SST and Chl *a* throughout the year suggesting that the satellite-derived SST data (abundant, easy to obtain and more reliable) might be used as a rough proxy to infer the spatial (superficial) structure of different waters masses in SMG (particularly in winter when the satellite-derived Chl a data is fragmentary). In general, the seasonal variability of the monthly values of satellite-derived Chl *a* for the whole area of GSM show average concentrations during autumn-winter, a peak in early spring (September) and the lowest Chl *a* values during summer (Williams *et al.* 2012). This seasonal cycle of the SMG is characteristic of subtropical waters (Mann and Lazier 1996, Williams *et al.* 2012).

Comparisons between SST gradient maps and the fishing activity maps showed that the fishing fleet was concentrated over and near the area of the frontal system during summer (December to March), obtaining the highest CPUE of the Argentine hake in relatively deep waters. Since the Argentine hake is the most important resource for the local industry, the dispersion of the fleet in autumn could be due to a reduction in CPUE, which would encourage captains to seek better catches in other (shallower) areas. The dispersion of the fleet coincides with the dissipation of the front, suggesting that the distribution and shoaling of the Argentine hake is associated with the presence of this tidal front. The explanation could be that the fronts increase the vertical mixing of water (Mann & Lazier 1996), resulting in increased primary productivity and, in some cases, in the activity of higher trophic levels (Olson & Backus 1985; Acha *et al.* 2004). Moreover, considering that adult hake feed actively after spawning (Hart 1946 *sensu* Podestá 1989), the formation of the front probably allows dense shoals to feed after the spawning season, recovering energy and the lipids reserves used during the reproductive season (Angelescu & Prenski 1987).

As mentioned before, the fleet remained dispersed in relatively shallow areas in autumn-winter, until the abrupt increase in catches of silver warehou *Seriolella porosa* in deep waters in the north of the gulf. The silver warehou is a typically pelagic and coastal species that is rarely found below 100 meters depth (Cousseau & Perrota 2004). This species has become the second important species in landings since 1998, due to a combination of seasonal appearance of dense shoals and commercial opportunities (Romero 2011). In this study, an increase in the number of hauls was observed between August and September, because fishermen performed night hauls to take advantage of the abundance of the silver warehou (Ocampo Reinaldo, 2010). Unfortunately, there is a lack of information about the biology and ecology of this species. The causes of the seasonal occurrence of the silver warehou within the gulf, as well as its apparent disappearance in late September remains unknown. The massive shoaling of the silver warehou seems to be related to a reproductive response (Ocampo Reinaldo, 2010) and not to the environmental features analysed in this study. Related to this, the statistical dependence between $CPUE_{sm}$ (constituted mainly by silver warehou) and SST gradients during August and September, could be explained by a large number of pixels with a combination of “Low gradients” and “High $CPUE_{sm}$” (Figure 9).

The “other species” group did not show significant variations throughout the year and the slight increase in winter yields may be due to: 1) a greater diversity of fish species in winter fishing areas (shallow waters), or 2) fishermen found a better commercial use of the bycatch, because of a lack of target species.

The oceanographic processes observed in this study allow us to infer some aspects of the spatial patterns of the Argentine hake. The winter decreases in CPUE may be explained by the dispersion of individuals (searching for food) throughout the water column in response to the absence of an environmental structure of the water. Moreover, some pelagic species are important prey in the diet of the Argentine hake of all sizes (e.g. Euphausiidae and anchovy *Engraulis anchoita* Hubbs & Marini, 1935; Ocampo Reinaldo *et al.* 2011) and prey aggregations can be related to surface environmental parameters (Alemany *et al.* 2009; Spinelli *et al.* 2012), thus the distribution of hake may be coupled, in part, with the distribution of their prey.

It is widely known that fish larvae should hatch into a realm with appropriate food and benign abiotic conditions (Hjort 1914; Cushing 1975, Lasker 1975; Bakun 1996; Gotceitas *et al.* 1996; Bakun & Csirke 1998). Moreover, the timing of spawning is decisive, particularly in areas with large seasonal changes in temperature and daylight hours (Wooton 1998). The spawning of the Argentine hake coincides with the seasonal structure of the water masses (warmer and stratified waters) in the northern area of SMG, which creates positive conditions to concentrate food, serving as favourable first-feeding sites for fish larvae (Bakun 1996). Therefore, the thermocline and environmental conditions should contribute to the timing of spawning of Argentine hake (González *et al*. 2010), and these areas could act as holding areas for eggs and larvae enhancing the reproductive success (Iles and Sinclair 1982; Macchi *et al*. 2004). Accordingly, the formation of the thermal front and the environmental patterns observed in this study may lead and modulate the reproductive strategy of the Argentine hake in SMG and the successful retention of hake recruits. In addition, the general circulation pattern of SMG in spring-summer is dominated by a cyclonic gyre, located at the northern half of the basin (Piola & Scasso 1998), which, in combination with the frontal system, determines the relative isolation of the northern water masses. The relative isolation of the northern waters contributes to the retention up to 40% of pelagic particles in the pelagic dominion over 250 days (Tonini 2010). This phenomenon may promote the retention of eggs and larvae of hake, as well as other planktonic organisms on the basis of the trophic chains (i.e. Euphausiidae), which are the main source of food for fish at larval and post-larval stages (Spinelli *et al.* 2012). Overall, the oceanographic characteristics of SMG seem to explain the summer distribution pattern of the Argentine hake, which may adapt its reproductive strategy and foraging behaviour to the cyclic environmental processes observed in the gulf. In contrast, on the ACS (outside the SMG), the "northern stock" spawns over the entire year, with peaks of activity from May to July (Rodrigues & Macchi 2010), whereas the "Patagonian stock" spawns from November to March, with peaks in January (Macchi *et al.* 2004). In upwelling zones, the Chilean hake *Merluccius gayi*, for example, spawns in association with frontal structures to enhance offspring survival (Vargas & Castro 2001), whereas the drift patterns of early larvae of the European hake *Merluccius merluccius* are a consequence of the local hydrographical processes (Alvarez *et al.* 2001; Olivar *et al.* 2003). In this respect, the duration of the pelagic larval phase of the Argentine hake is around 65 days (Buratti & Santos 2010). Therefore, the timing of spawning, the oceanographic phenomena and the topography observed in SMG seem to explain the isolation of this stock, supporting various new hypotheses about the importance of the Patagonian gulfs in the conservation of the aquatic resources (Machado Schiaffino *et al.* 2011).

Tidal fronts are relatively short temporal scale systems, which have been shown to have a stronger influence on fish diversity, biomass and assemblage structure than permanent frontal areas (Alemany *et al.* 2009). Accordingly, our results showed that the absence of a water mass structure in cold months does not promote the shoaling of hake, which is reflected in the dispersal of the fishing fleet and low landings. Considering that there is a seasonal ban that protects the reproductive process of hake, it is interesting to point out that the fleet captured a higher proportion of females in gonadal recovery stage in the warm months (after the seasonal ban, outside the closure area), obtaining the highest CPUE of the year. Although the winter catches showed mainly males and a low CPUE, the intense summer fishing may result in a high impact on the female population. This information is relevant to the design of new management tools (e.g. closures over the frontal zone or effort restrictions in summer) intended to provide biological sustainability to the Argentine hake fishery. It has been proposed that the ability of a population to rebuild itself in a closed area may depend on the fishing effort in that area before the closure (Babcock *et al.* 2005). However, it is also important to consider the effect of the displaced effort and, particularly in SMG, the seasonal concentration of fishing effort in the front area over segregated shoals of female hake.

Remote sensors are excellent tools to complement biological information with large-scale environmental information (Platt *et al.* 2007; Stuart *et al.* 2011). Vessel Monitoring System data are appropriate for mapping the large-scale distribution of fishing effort and the area impacted (Gerritsen & Lordan 2011; Skaar *et al.* 2011; Saitoh *et al.* 2011). In this study, a generalized approach (VMS and landing records) was used to identify the areas of SMG where trawlers seasonally operate and to analyse the potential relationships between abundance of the species captured and oceanographic processes.

Future research should focus in obtaining more *in situ* data about the seasonal distribution and abundance of species of intermediate trophic levels, as well as data of primary production, consumption and trophic relationships in the area of the frontal system. This information will contribute to a better understanding of the ecological processes that underlie the observed relationships between the physical ecosystem and fishery resources. Finally, the spatial management could be an interesting complementary tool and may enhance the expected effects of non-spatial strategies, helping to prevent biases in trends caused by spatial heterogeneity of populations and communities (Babcock *et al.* 2005), and supporting the gradual development of ecosystem-based fishery management.

Acknowledgements

The authors thank M. Sapoznik and N. Pérez de la Torre for their assistance in the processing of satellite images; P. Osovnikar and M. Maggioni for logistics of sampling; Cesar García and Ingrid Teich for their assistance in the spatial analyses and anonymous referees for their critical reviews and suggested changes to the manuscript. M.O.R., G.W, L.S and M.A.R. were supported by fellowships of CONICET (Argentina) and the work was partially supported by the projects PID 2003 371 and PICT 2006 1575 (ANPCyT, Argentina).

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TABLES

Table 1: Images free of clouds per month obtained from AVHRR (from 2004 to 2007) and SeaWiFS (from 2004 to 2006).

Month	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
AVHRR	12	25	33	15	31	19	36	39	39	35	36	18
SeaWiFS	4	2	2	6	16	15	12	11	23	16	13	10

Table 2: Categorized variables used in the test of independency. The pixels with SST gradients >0.1 in the SMG have been described as "frontal pixels" (Williams et al. 2010).

Categories	**SST gradients**	**$CPUE_{sm}$**
High	>0.1	>1000
Medium	0.05-0.1	500-1000
Low	<0.05	<500

Table 3: Results of the Partial Mantel test (Euclidean distance, 999 permutations, Bonferroni's corrected α=0.0084). The variables used to calculate the first and second distance matrix are shown. The third distance matrix used in all analyses was based in the geographical position of each pixel. Significant tests are shown in bold and p values between parentheses.

Autumn/Winter	**SST**	**Chl *a***	**SST_{grad}**	**$CPUE_{sm}$**	***Spring/Summer***
SST		***0.7885*** *(0.001)*	***0.1731*** *(0.001)*	***0.01937*** *(0.005)*	***SST***
Chl *a*	**0.1854** (0.001)		***0.2118*** *(0.001)*	*0.0084 (0.069)*	***Chl a***
SST_{grad}	**0.2622** (0.001)	-0.0482 (1)		***0.1102*** *(0.001)*	***SST_{grad}***
$CPUE_{sm}$	-0.04173 (1)	0.0011 (0.406)	-0.1019 (1)		***$CPUE_{sm}$***

Table 4: Results of the Pearson χ2 test of independency between CPUEsm and SST gradients (3x3 table, Bonferroni's corrected α=0.0042). Significant tests are shown in bold.

Month	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
χ^2 Pearson	11,77	6,46	11,28	**47,48**	**63,48**	**19,58**	**194,86**	**28,96**	**49.49**	**209,71**	**122,15**	**32,57**
p	0,0191	0,1676	0,0236	<0,0001	<0,0001	0,0006	<0,0001	<0,0001	<0,0001	<0,0001	<0,0001	<0,0001

FIGURE CAPTIONS

Figure 1: Location of the three stocks of Merluccius hubbsi in Argentine waters. There are 2 closure areas for trawlers in SMG (Río Negro Province): a seasonal one from October to November at north of parallel 41°30'S, and a permanent one (small polygon), which is an area reserved for artisanal longliners. The figure shows the relative position of the tidal front and the general circulation in the basin during summer. The big polygon (dotted line) shows the area sampled for the statistical analyses. NS: Northern stock; PS: Patagonian stock.

Figure 2: Monthly climatological maps and fishing activity maps of the SMG. a) SST; b) SST gradients, c) Chl a, d) fishing activity.

Figure 3: Frequency of fishing activity records from the SiMPO respect to the duration of the hauls registered by the FOP. 0: False negative (The SiMPO failure to register the fishing activity). 1, 2, 3: Indicate the number of SiMPO records per haul. The z-axis labels were rearranged to facilitate interpretation.

Figure 4: Frequency distribution of the fishing depths of the SiMPO registers. The letters (a, b) indicate months without statistical differences between them (Kolmogorov-Smirnov, α=0.05). ad: Average depth; se: standard error.

Figure 5: Monthly CPUE of Merluccius hubbsi, Seriolella porosa and other species, grouped from 2004 to 2007. The largest effort (dotted line) was registered in August and September, because the fleet added additional night hauls to catch more silver warehou.

Figura 6: Average proportion of sexes in the catch of Merluccius hubbsi (number of females/number of males) per month, grouped for the years 2004 to 2007. Months have been distinguished with the presence of seasonal thermal front. The x-axis labels indicate the month of capture, the total number of individuals sampled and the number of hauls from which these individuals have been obtained.

Figure 7: Gonadal stages of mature females of Merluccius hubbsi (>27 cm of total length) in monthly catches of the industrial fleet. The x-axis labels indicate the month of capture, the total number of individuals sampled and the number of hauls from which these individuals have been obtained. 1, 2, 3 and 4: Pre-spawning stages; 5: spawning, 6 and 7: post-spawning and gonadal recovery.

Figure 8: Hepatosomatic Index (HSI) of mature females of Merluccius hubbsi (>27 cm of total length) in the catches of the industrial fleet. The x-axis labels indicate the month of capture, the total number of individuals sampled and the number of hauls from which these individuals have been obtained.

Figure 9: Colour-coded pixels by CPUEsm and Gradients. In order to illustrate each season, are shown only the months of February (late spring-summer, an example of the “hake season”), May (autumn, “other species season”) and September (winter- early spring, “silver warehou season”). In September several pixels (purple) with a combination of “High CPUEsm” and “Low Gradients” were found. In this month “High Gradients” pixels were not found, in consequence, the combination (high gradients-low CPUEsm) was not possible.

FIGURES

Figure 1

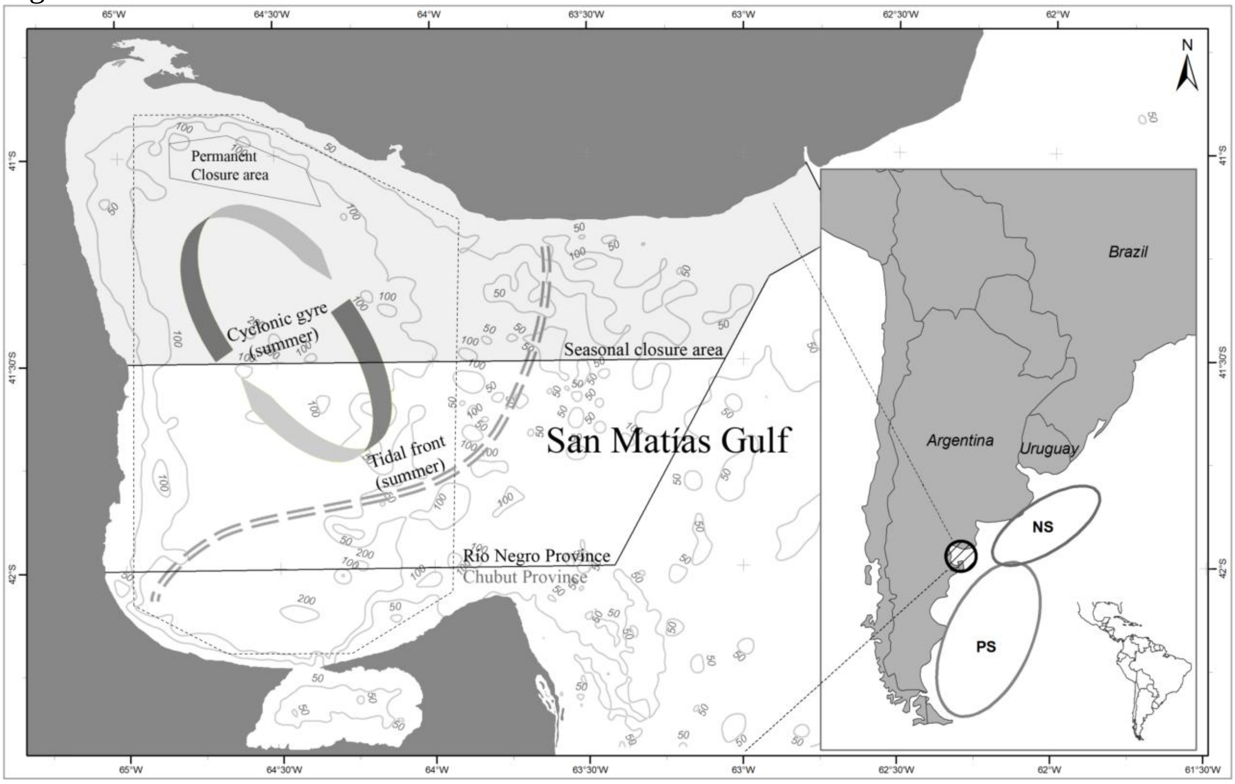
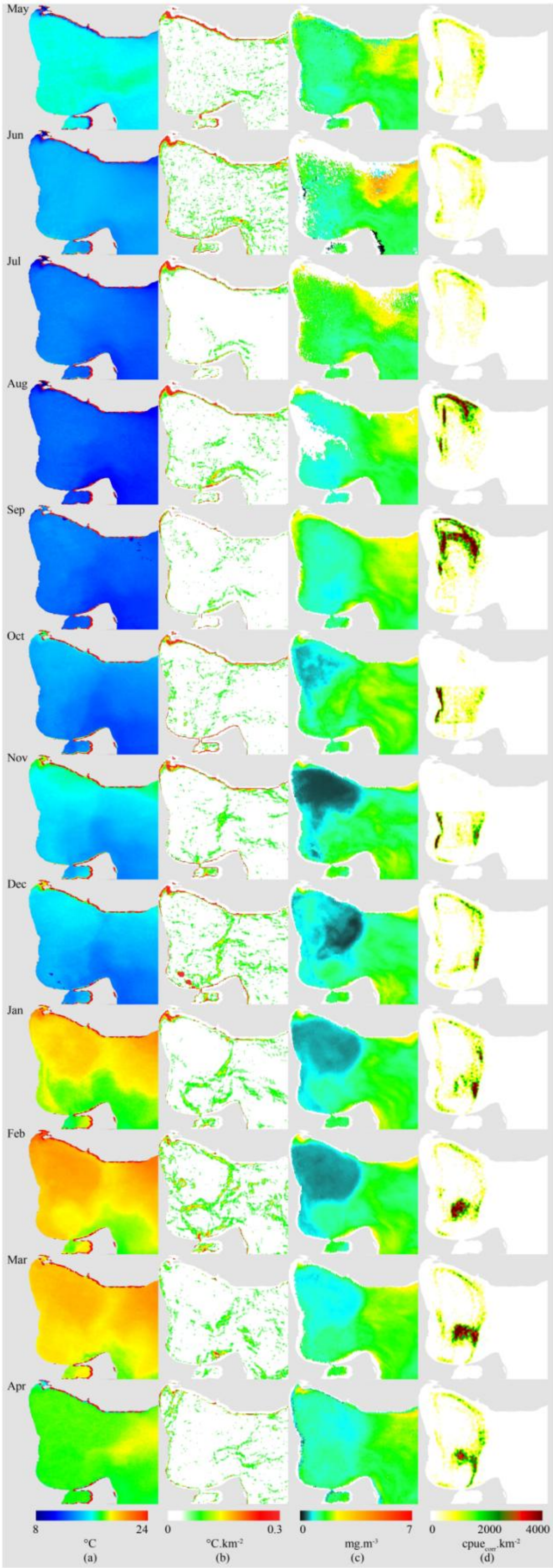


Figure 2


May
Jun
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8
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°C
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0
7
mg.m-3
(c)
0
2000
4000
cpuecorr.km-2
(d)

Figure 3

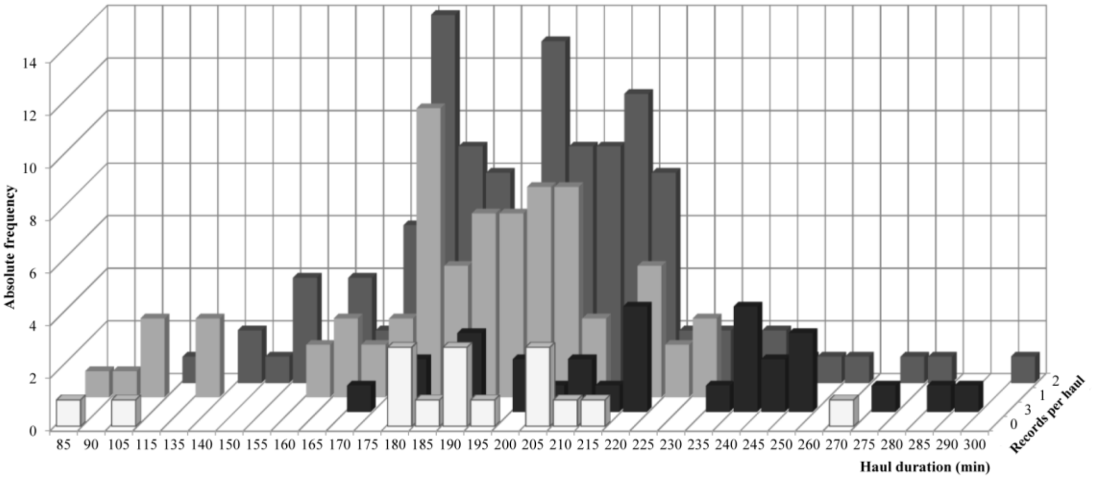


Figure 4

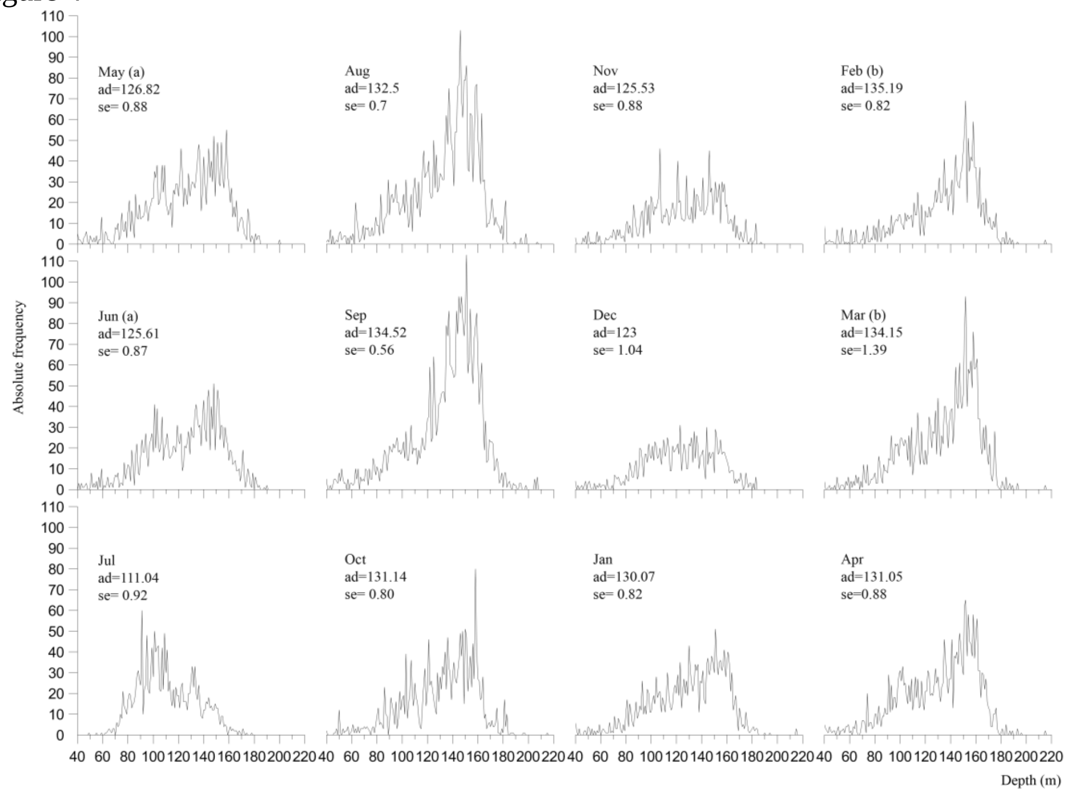


Figure 5

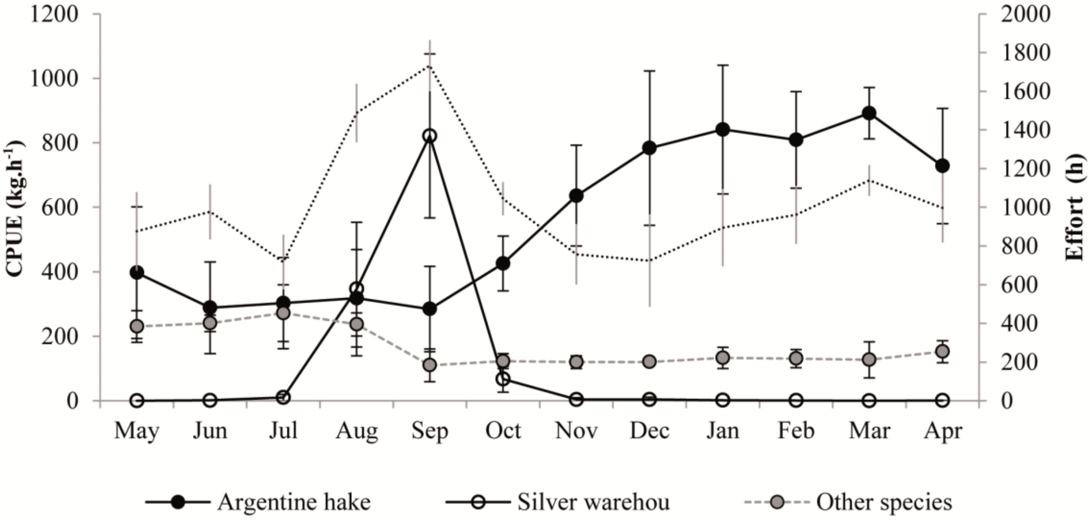


Figure 6

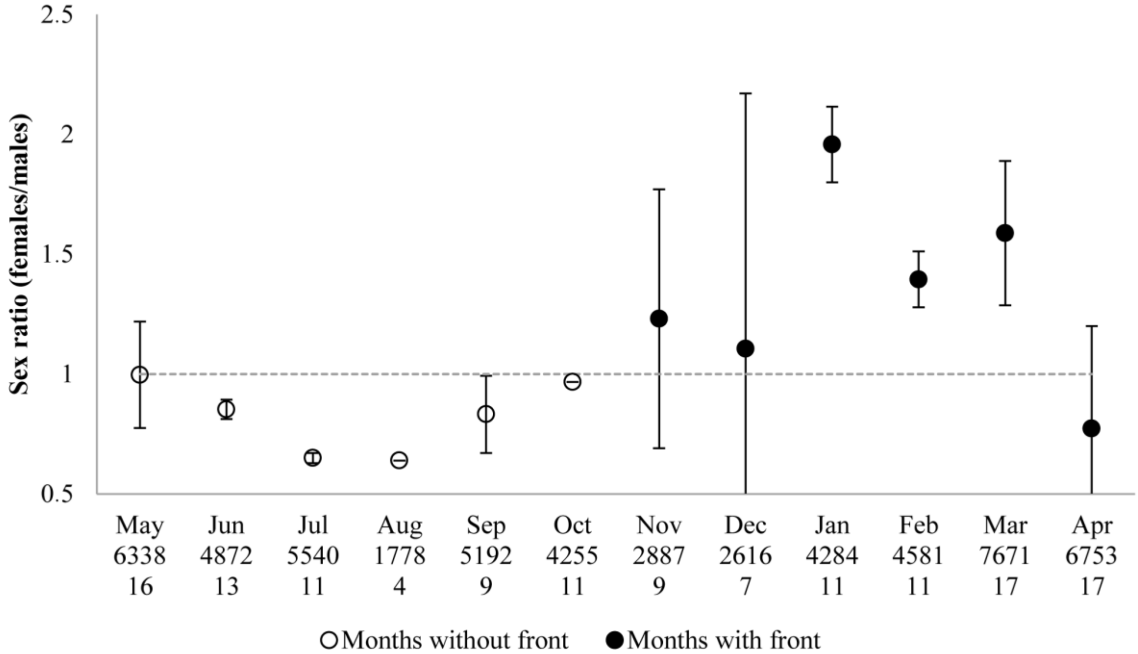


Figure 7

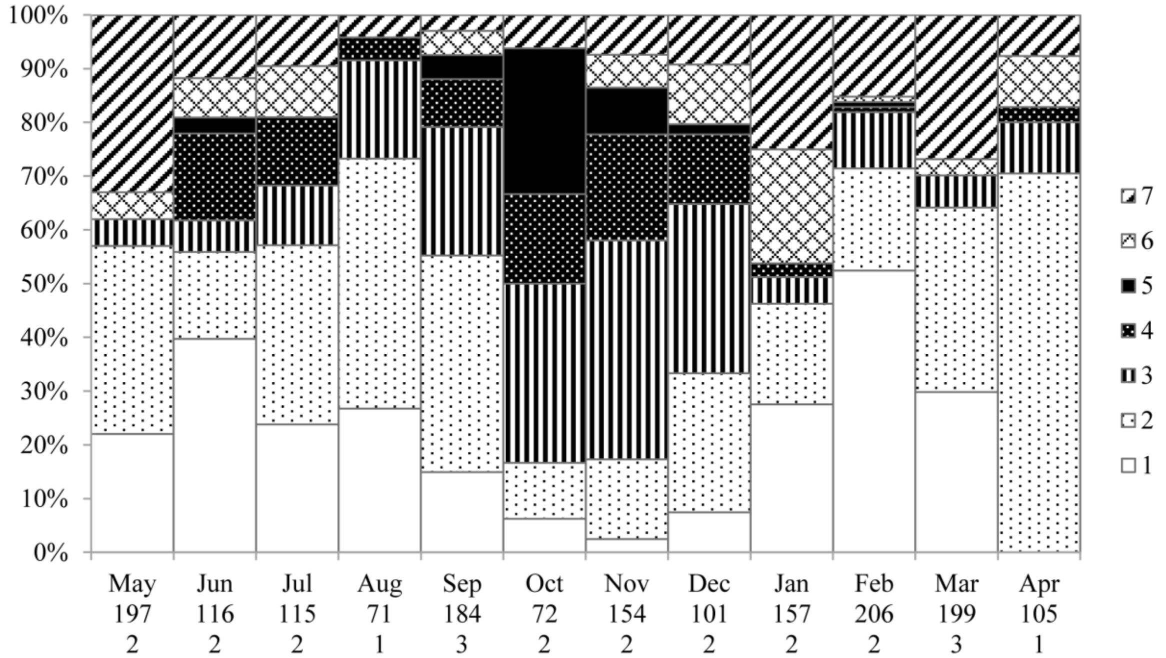


Figure 8

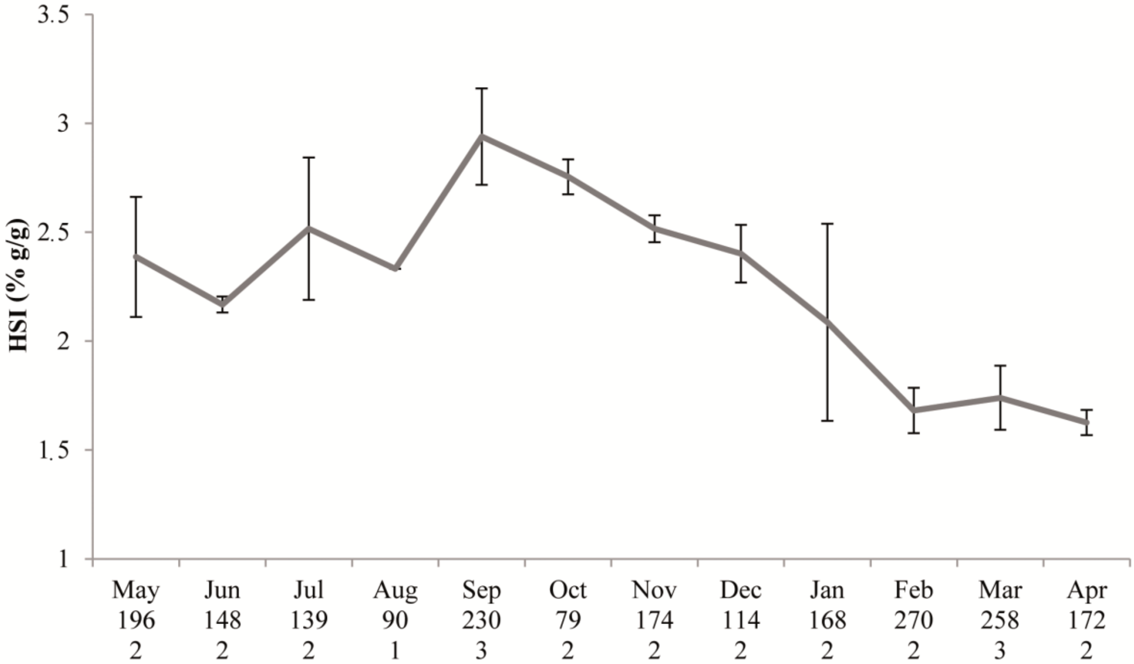
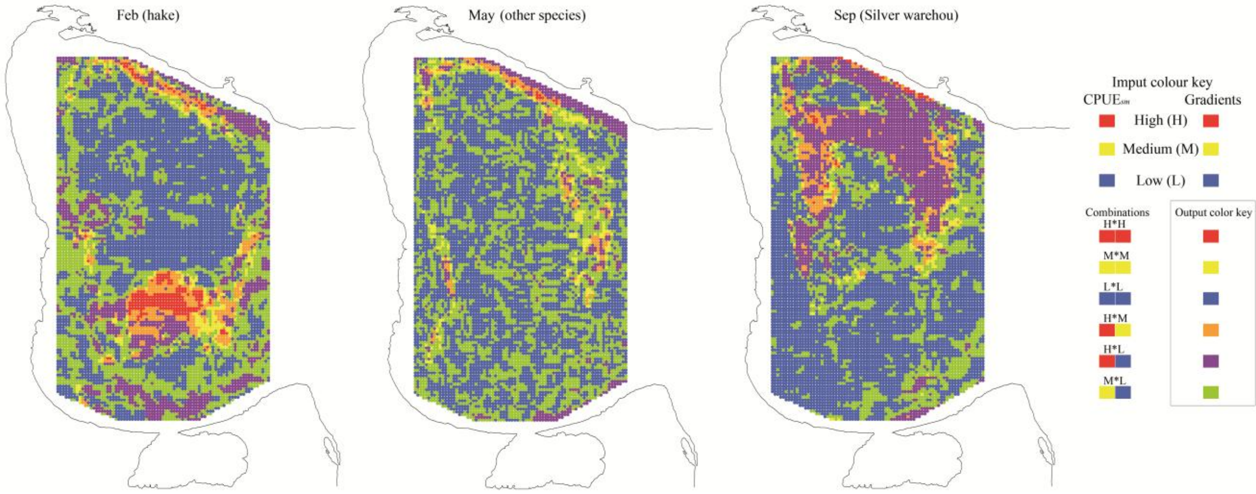


Figure 9



Feb (hake)
May (other species)
Sep (Silver warehou)
Imput colour key
CPUE
Gradients
High (H)
Medium (M)
Low (L)
Combinations
H*H
M*M
L*L
H*M
H*L
M*L
Output color key