Habitat expansion and contraction in anchovy and sardine populations

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ABSTRACT

We investigated the relationships between stock biomass, distribution area and mean density of sardine and anchovy populations off California, Peru, South Africa and Japan. Our objective was to elucidate whether their ecological responses to habitat availability and use would support the possibility of them developing synchronic, alternating biomass fluctuations. Results indicate that as populations of both species grow in size, both the area they occupy and their packing density increase, generally consistent with the basin model. The relationship between distribution area and stock biomass is allometric, which implies that there is a limit to the stock expansion to new areas. Patterns of space occupation appear to differ between sardine and anchovy in some regions. In South Africa and Japan anchovy occupies larger area per unit biomass than sardine, consistent with habitat requirements as determined by their feeding ecology. Off California and Peru results confirm that in general species expand their distribution area with stock size, but specific patterns are less clear. Reasons for this are discussed, including sampling biases, the role of upwelling in limiting anchovy's habitat off Peru, the ability of sardine to use offshore habitats off California, as well as possible differential space occupation patterns during population growth and decline. It is suggested that habitat availability may not be a pre-requisite for sardine growth in some areas, while anchovy may require habitat to become available for populations to grow. The differential habitat dependency and use of space between both species suggests that they cannot be considered to ecologically replace each other. While differences in space utilization may provide opportunities for diverging population paths, the ecological mechanisms behind out-of-phase fluctuations may be much more complex than a simple replacement. The results provide the first comparative, quantitative estimates of biomass/area relationships for pelagic fish, of use in models investigating the potential for expansion and contraction of anchovy and sardine populations worldwide based on climate change-driven habitat predictions.

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1. Introduction

Small pelagic fish species are economically and ecologically important components of many marine ecosystems, particularly in upwelling regions. They contribute approximately a third of the global fish catch (FAO, 2007) and play a critical role in the transfer of energy from lower to higher trophic levels (Cury et al., 2000). Small pelagic fish species are short lived and fast growing and are characterized by marked fluctuations in their stock size because of their high dependence on highly variable, environmentally-driven, annual recruitment pulses. There is evidence to suggest that these species also display low frequency, multi-decadal productivity cycles (Schwartzlose et al., 1999; Jacobson et al., 2001; Barange et al., 2009) (Fig. 1). It has also been argued that the productivity cycles of anchovy and sardine alternate (Klyashtorin, 1998; Lluch-Belda et al., 1989), perhaps linked to large-scale climate or oceanic forcing operating at the basin scale (Kawasaki, 1991; Lluch-Belda et al., 1989, 1992; Chavez et al., 2003). However, the evidence for alternate productivity cycles is contested (Baumgartner et al., 1992; Fréon et al., 2003). Clarifying the existence of such out-of-phase production cycles has important consequences. De Oliveira (2006) investigated different harvesting strategies in South Africa fishery for sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) and concluded that, if out-of-phase sinusoidal trends exist, management procedures designed under such an assumption could be more effective than traditional approaches.

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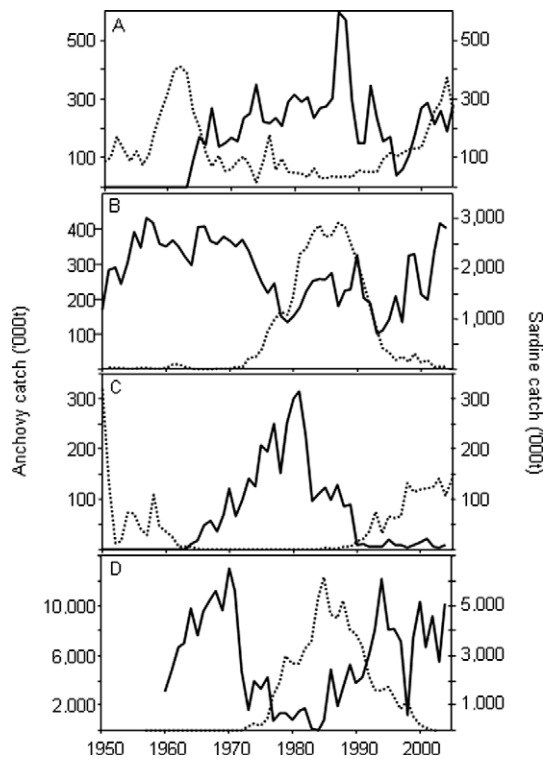E-mail address: m.barange@pml.ac.uk (M. Barange).

Fig. 1. Landings of anchovy (solid line) and sardine (dotted line) in South Africa (A), Japan (B), California (C) and Peru (D). Data from Barange et al. (2009).

Several hypotheses have been proposed to explain out-of-phase abundance fluctuations in anchovy and sardine populations. Lluch-Belda et al. (1992) concluded that shifts in global atmospheric and sea temperatures coincide with productivity cycles, but accepted that the mechanistic link may be caused by an associated process or event operating at regional level. Chavez et al. (2003) concluded that the Pacific had a regime oscillation periodicity of approximately 50 years, affecting atmospheric pressure systems, sea level, ocean circulation patterns, oceanic mixed layer, and from there alternative food web dynamics favouring one or another species. It also indicated that the warming (cooling) in the eastern Pacific is out-of-phase with the central North and South Pacific. Takasuka et al. (2007) proposed a simple "optimal growth temperature" hypothesis, in which anchovy and sardine regime shifts are caused by differential optimal temperatures for growth during the early life stages. This hypothesis is an extension of the "optimal environmental window" theory (Cury and Roy, 1989), which established that moderate upwelling intensity was favourable for recruitment. The optimal growth temperature hypothesis also addresses why fish cycles can be synchronous on both sides of an ocean basin, when the atmospheric forcing is reversed, by claiming that optimal temperatures for both species can also be reversed (Takasuka et al., 2008). An alternative hypothesis establishes that such fluctuations may be trophodynamically mediated. Van der Lingen et al. (2006) used compelling evidence of size-based resource partitioning, based on morphological differences in anchovy and sardine feeding apparatus, to hypothesise that species alternations are likely to be based on competition and adaptation to specific food resources. This trophodynamic hypothesis links shifts in physical ocean regime and plankton community to shifts in dominance of anchovy and sardine based on the bottom-up pathway.

The above hypotheses focus on different scales or factors but are theoretically non-exclusive and synergistic, and they suggest that anchovy and sardine may respond in opposite ways to external forcing, as if they were ecological congener species which com-

pete for habitat and resources. In this paper we explore the strategies of habitat use in both species, to test the hypothesis that ecological congener species would demonstrate similar ecological responses to habitat availability and use.

It is generally agreed that habitat selection in marine fish is based on the "ideal free distribution" (Fretwell and Lucas, 1970), according to which habitat choice is based on suitability and geared towards maximising individual fitness. For some authors habitat suitability is density-dependent, leading to the prediction that the geographical area occupied by a population expands as population size increases and contracts as it declines (Paloheimo and Dickie, 1964; MacCall, 1990; Bertrand et al., 2004). Decrease in occupied area at low stock abundance has certainly been reported for some demersal fish species (Swain and Wade, 1993; Marshall and Frank, 1995; Atkinson et al., 1997; Myers and Stokes, 1989; Swain and Sinclair, 1994; Myers and Cadigan, 1995; Swain and Benoit, 2006), but not for others (Swain and Morin, 1996; Murawski and Finn, 1988; Petitgas, 1998). Some schooling pelagic fishes are known to occupy less area at low stock sizes (e.g. Barange et al., 1999), resulting in an increase in catchability (MacCall, 1976; Ulltang, 1980; Winters and Wheeler, 1985; Csirke, 1989). Density-independence has also been invoked to explain changes in habitat suitability. Because individuals are unlikely to have the freedom of movement to detect habitat conditions beyond their perceptual range, Shepherd and Litvak (2004) conclude that density-dependent habitat selection is probably only important at relatively small scales, and that the importance of density versus environmental dependence is influenced by the spatial scale of the analysis (cf. Bertrand et al., 2008). For example, Swartzman et al. (2008) showed that Peruvian anchovy (*Engraulis ringens*) is restricted to upwelled cold coastal waters independent of its abundance, as suggested by the habitat-based model proposed by Bertrand et al. (2004). In addition, Rodriguez-Sanchez et al. (2002) argued that during high biomass periods sardine (*S. sagax caerulea*) off California expands its distribution area outside the area occupied during low biomass periods, implying both density-dependent and density-independent habitat control mechanisms.

These observations can be summarized into three basic models that describe the relationship between stock size, distribution area and local density (Petitgas, 1998): (i) constant density model, where density stays constant and the area covered by the stock varies with abundance (Iles and Sinclair, 1982; Hilborn and Walters, 1992); (ii) proportional model, where the area occupied stays constant and local density varies proportionally to abundance (Houghton, 1987; Myers and Stokes, 1989; Hilborn and Walters, 1992; Petitgas, 1997); and (iii) basin model, where density and area vary with abundance (MacCall, 1990). Petitgas (1998) proposed a modified version of the basin model, where only some local areas change their density with population abundance.

If anchovy and sardine behave like congener species demonstrating synchronic, out-of-phase, basin-scale abundance fluctuations, then their ecological responses to habitat availability and use should also be equivalent. However, this hypothesis has not been tested and evidence in its support is currently lacking. Species-specific differences in the occupation of space between sardine and anchovy have been observed in South Africa (Barange et al., 2005) and Japan (Oozeki et al., 2007). Bertrand et al. (2004) reported differential exploitation of habitat loopholes by both species as a way of responding to El Niño events off Peru. These observations may seem inconsistent with the concept of equivalent habitat selection patterns between both species; however, unequivocal information is missing.

In this contribution we compare the relationships between annual stock biomass, distribution area and mean density of sardine and anchovy populations off South Africa, Japan (Kuroshio Current), California and Peru (Humboldt Current), with the objec-

tive of elucidating whether their habitat selection strategies support the possibility of them developing synchronic, alternating biomass fluctuations.

2. Material and methods

Data for this exercise comes from sardine and anchovy monitoring surveys, conducted as part of their management needs in the four regions considered.

South African data come from standard hydro-acoustic surveys conducted off South Africa in the Austral summer (1984–2007) to estimate the biomass and distribution of anchovy (*E. encrasicolus*) and sardine (*S. sagax*). Details of the surveys, sampling strategy and data collected are available elsewhere (Hampton, 1987, 1992; Barange et al., 1999). Spawning products were obtained at regularly spaced stations along the survey transects using a CalVET net hauled from 100 m depth (or 5 m from the bottom) to the surface. Egg and adult fish distribution maps were obtained from interpolating acoustic (adult) and CalVET (egg) density data using standard Kriging routines (Barange and Hampton, 1997; Barange et al., 1999). Surface area covered by fish densities >1 g m^{-2} (or > 1 egg m^{-2}) were computed from adult and egg distribution maps of both species using SURFER$^{©}$. Fish biomass data used in this contribution are updates of the historical time series as described in Coetzee et al. (2008a). They differ from previously published data (e.g. Barange et al., 1999) in two aspects. First, *in situ* estimates of acoustic target strength for both species have now been applied, accounting for the different reflectivity properties of anchovy and sardine (Barange et al., 1996). Second, hydro-acoustic systems have been upgraded regularly through the duration of the time series, each differing in terms of acoustic receiver saturation levels. Current figures have been corrected to account for receiver saturation and are thus fully comparable (see Coetzee et al., 2008a for details). Age-structured production models are used to assess these stocks, using the acoustic estimates of anchovy spawning stock biomass (SSB) as relative indices of abundance and of total biomass for sardine as absolute indices.

Egg and larval surveys along the Pacific coast of Japan have historically been conducted since 1947. The survey areas covered the major spawning grounds of Japanese anchovy (*Engraulis japonicus*) and sardine (*Sardinops melanostictus*) off the Pacific coast. Surveys reported on in this contribution were conducted monthly from 1978 to 2004, with more intense sampling during early spring. Egg and larval samples were obtained using vertical tows of a net with 0.33 mm or 0.335 mm mesh size from 150 m depth (or just above the bottom) to the surface. Monthly egg abundances were calculated for each 15′ latitude × 15′ longitude square. Calculation procedures are explained in Oozeki et al. (2007) and summarized as follows. First, the number of eggs was standardized to densities per unit area. Egg density for each 15′ × 15′ square was computed by arithmetically averaging egg densities of all tows conducted in the square for each month, considering temperature-dependent egg incubation time as well as survival rates (Nakai and Hattori, 1962). Mortality (survival rate) during egg stages was estimated from the decrease of the number of eggs by developmental stage using long-term datasets. Annual relationships between egg-based spawning area (based on densities computed during the peak spawning month of the two species, February for sardine and June for anchovy) and SSB (obtained through virtual population analysis), were examined.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) programme off California was initiated in the late 1940s to study the causes of the decline in the sardine (*S. sagax caerulea*) population. It is carried out by NOAA's National Marine Fisheries Service Southwest Fisheries Science Center, the California

Department of Fish and Game, and the Integrative Oceanography Division (IOD) at Scripps Institution of Oceanography (SIO). The first phase of the survey programme (1951–1960) included monthly surveys, while a second phase (1961–1965) included four surveys a year (January, April, July and October). While this periodicity was largely respected subsequently, some years had additional or alternative surveys in February, March and/or August. Surveys between 1964 and 1982 were particularly irregular due to the lack of sardine and competing demands for ship time. The geographic extent of the survey changed over time, with only a portion of the sampling grid measured consistently from 1951 to present (Smith, 1990; Ohman and Smith, 1995). The current analysis uses data from 1951 up to 2007. In order to ensure consistency with our approach in other areas of this study, data from the entire range of the survey was considered in this analysis. Ichthyoplankton samples were collected at all stations using bongo tows (oblique hauls reaching ~150 m depth), with a 1 m opening and 505 μm mesh and CalVET vertical hauls reaching ~70 m depth, with 0.25 m opening and 150 μm mesh. While CalVET are better suited to catching sardine eggs the bongo time series is longer. Estimates of spawning area have been computed using two methodologies, not entirely independent of each other. First, spawning areas were computed as part of the stock assessment procedures using all available information including bongo nets (oblique tows to 250 m), CalVET nets (vertical tows to 100 m), and CUFES (underway eggs sampling to 3 m). ArcGIS (ESRI) software was used to plot egg positions, egg distributions were encompassed using multiple complex polygons, and area occupied was summed in n.mi^2. Data using this method include the periods 1983–2007 for sardine and 1964–1995 for anchovy (*Engraulis mordax*). Second, planar areas in the month of peak spawning were computed by interpolating egg density data from CalCOFI surveys using standard Kriging routines and measuring the area covered by densities >1 egg m^{-2} (as was done for South African data) for April surveys. This month roughly coincides with the peak spawning of sardine, but not anchovy, that spawns through the year with a peak in late winter–spring. While this may indicate a potential bias against anchovy distribution area estimates, April still offered the best coverage in terms of average egg density and number of positive stations in the entire time series for both anchovy and sardine. The regression between these two areal calculations is statistically significant ($r = 0.87$ for sardine and $r = 0.94$ for anchovy, both $p < 0.001$), but the CalCOFI-based calculation offers a longer data set, and was therefore preferred unless stated. SSB estimates for anchovy (Jacobson et al., 1994) and sardine (Hill et al., 2007) are based on age-structured population models incorporating daily egg production method (Lo et al., 2005) time series of relative abundance.

The Peruvian Marine Research Institute (IMARPE) has collected hydro-acoustic data for anchovy (*E. ringens*) and sardine (*S. sagax*) off Peru since 1983 at a rate of approximately one survey per year between 1983 and 1995 (mostly in winter), and between three and four surveys per year since 1996 (winter, summer and sometimes autumn and spring). The surveys were designed to cover the distribution range of anchovy, but other species, such as sardine, are also recorded. The summer surveys are designed to assess the entire biomass of the anchovy stocks while winter surveys are used to estimate the biomass of the anchovy spawning stocks only, and cover a limited latitudinal range. However, all the surveys report total biomass, and no separation has been made here between spawners and non-spawners. Survey design and sampling procedures are available elsewhere (e.g. Simmonds and MacLennan, 2005; Gutierrez et al., 2007). For this paper data from 1983–2006 was used, but the survey area was limited to the region 5–15°S to standardise the data set. Distribution areas were computed from acoustically-derived species distribution maps following slightly different procedures over the duration of the time series. The most

common procedure is based on proportional abundance of the species in squares of 30′ of latitude for every 10 n.mi. from the coast (Gutierrez and Peraltilla, 1999). SSB estimates are obtained directly from acoustic surveys as well as from virtual population analysis that incorporate fisheries data (Simmonds et al., 2009).

The above information was used to produce biomass versus distribution area, and biomass versus packing density, the latter being computed as the ratio between the spawning stock biomass (SSB) and the distribution area for a given year. It must be noted though that "distribution area" in the South African and Peruvian datasets reflect fish distribution area at the time of spawning, while Japan and California data refer to the distribution area of spawning products during the month of peak spawning. Multifactor analysis of variance and regression analysis were used to test the significance of the results.

3. Results

3.1. Adult versus egg distribution areas

Estimates of distribution area are ideally measured from fish biomass surveys by mapping the area covered by adult fish, as conducted off South Africa and Peru. However, adult surveys are not available off Japan and California, where egg surveys are the basis for their monitoring programmes. In these cases egg distribution area is used as a proxy for adult fish distribution area. To make sure that both estimates are comparable we tested this assumption using data from South Africa, where concurrent egg and adult fish distribution areas are computed annually (Fig. 2). The results confirm that the distribution areas of adult fish and spawning products are comparable, both for anchovy ($r = 0.89$, $p < 0.001$) and for sardine ($r = 0.76$, $p < 0.001$). The results indicate that, if the egg samples are taken during the peak period of the species' spawning season, the distribution area of the eggs is proportional (but not equivalent) to that of the adults, thus validating the use of either eggs or adult to estimate the relationship between distribution area and size of the stock. While proportional, the area of distribution of eggs in the southern Benguela is roughly 1.5–3.5 times larger than that of the adults. This ratio is unlikely to be consistent between regions.

3.2. Biomass versus distribution area

Fig. 3 shows the relationship between population size (spawning stock biomass, SSB), and distribution area, for all regions and species. Analysis of variance of the whole data set (Table 1) indi-
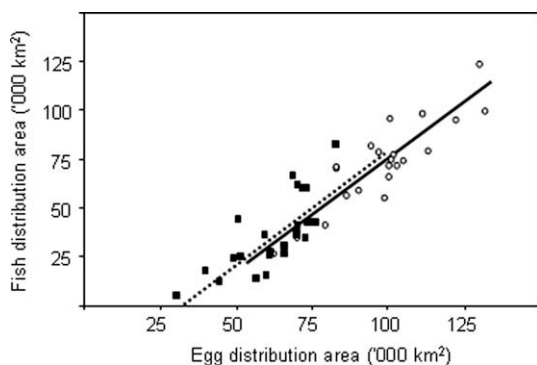

Fig. 2. Distribution area of eggs and adult anchovy (open circles, solid line) and sardine (closed squares, dotted line) off South Africa, from annual spawner biomass surveys, 1984–2007. Egg data comes from regularly-spaced CalVET net samples, while fish data come from hydro-acoustic records. Areas for both data sets were computed as described in Section 2.
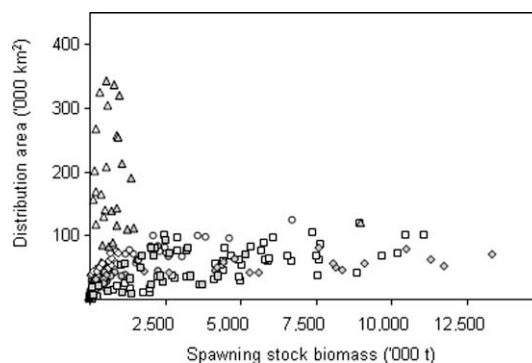

Fig. 3. Relationship between spawning stock biomass and distribution area of adult fish or spawning products, for South Africa (circles), Japan (diamonds), California (triangles) and Peru (squares) for anchovy (empty symbols) and sardine (filled symbols).

Table 1
Results of the analysis of variance of the area per unit of biomass according to region (South Africa, Japan, California and Peru) and species (anchovy and sardine).

Source	Sum squares	D.f.	F-ratio	P-value
Main effects				
Region	30.31	3	22.03	0.0000
Species	0.28	1	0.62	0.4334
Residual	107.78	235		

cates that the area occupied per unit biomass differs between regions, separating California data from the other three regions. Therefore, all further analysis will be separated between regions.

Within regions results consistently indicate that larger distribution area (A) is occupied with increasing population size (SSB) for both anchovy and sardine. However, differences are observed between species in some regions.

Off South Africa both anchovy ($A = 240.1 * SSB^{0.395}$; $r = 0.89$, $p < 0.001$) and sardine ($A = 51.8 * SSB^{0.478}$; $r = 0.90$, $p < 0.001$) showed clear relationships between SSBs and fish distribution areas, indicating that the stock expand and contract as a result of population fluctuations (Fig. 4). An analysis of variance indicates that the scale of this relationship is significantly different between species, but not its pattern (not significant interaction between biomass and species factors, Table 2). At average stock levels the anchovy stock tends to occupy approximately 40% more area per unit of biomass than sardine, and as a result the latter has larger packing densities than anchovy (Fig. 4).

Off Japan small pelagic stocks displayed similar trends to those off South Africa, with both sardine ($A = 272.08 * SSB^{0.3381}$; $r = 0.91$, $p < 0.001$) and anchovy ($A = 2140.3 * SSB^{0.2466}$; $r = 0.82$, $p < 0.001$) demonstrating clear relationships between SSB and spawning area (Fig. 5). A significant interaction between parameters in the analysis of variance (Table 2) indicates that the pattern of space occupation per unit of biomass is significantly different between both species. In this case area (A) reflects the distribution of eggs in the peak spawning month. Assuming that the distribution of spawning products is related to the distribution of adult fish (Fig. 2) the regressions would indicate that at a stock size of approximately 2 Mt sardine would occupy on average 50% less space than anchovy at the same stock level, as reflected in their differential packing densities (Fig. 5).

The relationship between SSB and spawning area off California is noisier than off Japan and South Africa, possibly because of differences in CalCOFI survey coverage, as discussed later (Hewitt, 1988; Smith, 1990; Ohman and Smith, 1995). Patterns are still consistent with the hypothesis that egg distribution area increases
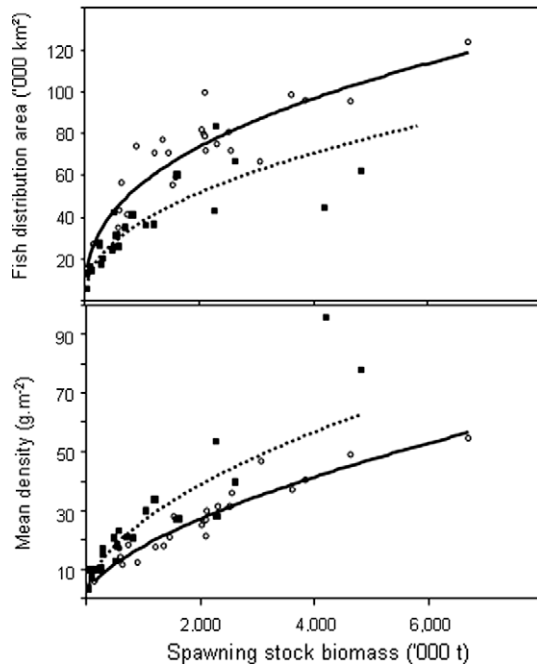
Fig. 4. Relationship between anchovy (open circles, solid line) and sardine (closed squares, dotted line) spawning stock biomass, fish distribution area (top panel) and average packing density (bottom panel), off South Africa (1984–2007).

Fig. 5. Relationship between anchovy (open circles, solid line) and sardine (closed squares, dotted line) spawning stock biomass, egg distribution area (top panel) and average packing density (bottom panel, assuming that the egg distribution area reflects the distribution of adult fish, Fig. 2), off Japan (1978–2004). Distribution area computed on the peak spawning month, February for sardine and June for anchovy (from Oozeki et al., 2007).

with biomass, but there is no indication of a difference in distribution area or density between both species (Table 2, Fig. 6). Using sardine data only, a significant regression is obtained ($A = 994.0 * SSB^{0.3601}$; $r = 0.65$, $p < 0.001$, Fig. 6).

Off Peru the relationship between spawning biomass and spawning area is also confirmed. The relationship is not significantly different between anchovy ($y = 17.38x^{0.5273}$, $r = 0.84$,
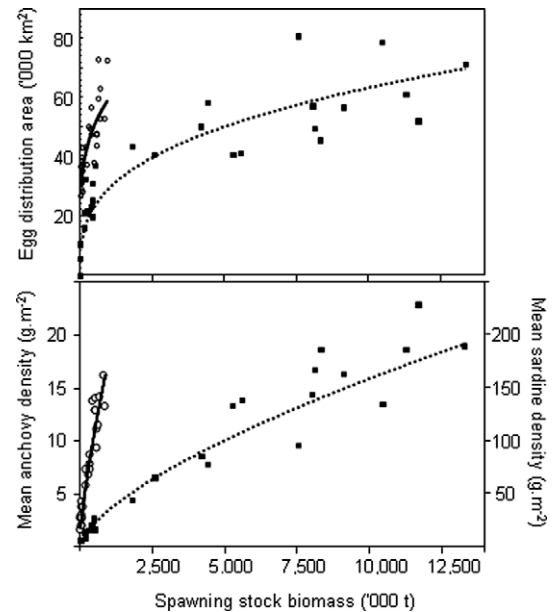
Table 2
Results of the analysis of variance of the regression between area (dependent variable) and biomass (independent variable), by region and species. Bold values indicate significance at $p < 0.05$. California data limited to the periods 1983–2007 for sardine and 1964–1995 for anchovy (see Section 2).

| Region	Parameter	T-statistic	P-value
South Africa	Constant	9.588	**0.0000**
	Biomass	6.944	**0.0000**
	Species	−3.729	**0.0005**
	Biomass * species	−0.589	0.5582
	Durbin–Watson statistic	1.716	0.0852
	r Adjusted for d.f.	0.88	
Japan	Constant	10.177	**0.0000**
	Biomass	5.670	**0.0000**
	Species	−2.085	**0.0421**
	Biomass * species	−5.045	**0.0000**
	Durbin–Watson statistic	1.2384	**0.0004**
	r Adjusted for d.f.	0.84%	
California	Constant	1.8022	0.0785
	Biomass	2.09887	**0.0417**
	Species	−0.9963	0.3247
	Biomass * species	−0.31057	0.7576
	Durbin–Watson statistic	0.5113	**0.0000**
	r Adjusted for d.f.	0.55%	
Peru	Constant	3.1769	**0.0022**
	Biomass	5.4391	**0.0000**
	Species	−1.0192	0.3114
	Biomass * species	2.1171	**0.0376**
	Durbin–Watson statistic	0.7948	**0.0000**
	r Adjusted for d.f.	0.68%	
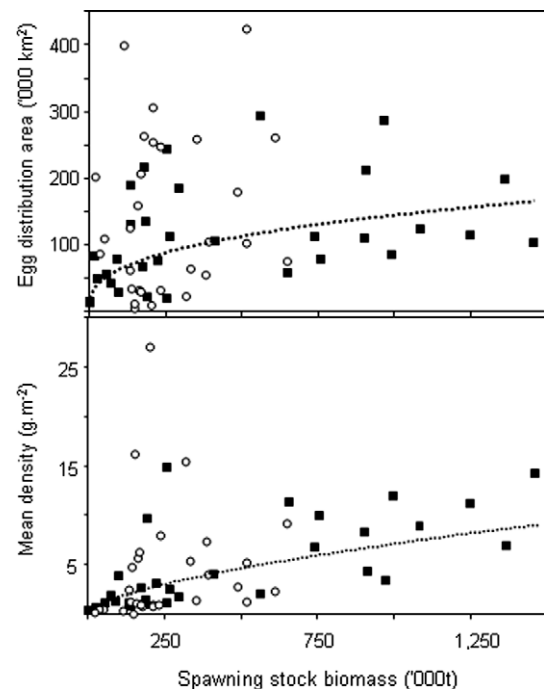
Fig. 6. Relationship between anchovy (open circles, 1954–1995) and sardine (closed squares, dotted line, 1951–2007) spawning stock biomass, egg distribution area (top panel) and average packing density (bottom panel, assuming that the egg distribution area reflects the distribution of adult fish, Fig. 2), off California. Distribution area computed from April surveys. No regression line is shown for anchovy due to lack of statistical significance.

$p < 0.001$) and sardine ($y = 0.846x^{0.7176}$, $r = 0.72$, $p < 0.001$) (Fig. 7, Table 2), although individual species equations are provided for comparative purposes. It can be observed that the packing density

per year varies considerably within species but not between species (Fig. 7), as a result of the large variability in the data.

3.3. Biomass versus distribution area during population growth and decline

The length of the time series from California and Japan allows for a more detailed analysis of the relationship between SSB and spawning area by separating the data between periods of population growth and decline (data from Barange et al., 2009). Off Japan (Fig. 8, Table 3), sardine occupies a larger area per unit of biomass during stock decline (period 1990–2004; $y = 67.58 * SSB^{0.4517}$; $r = 0.91$, $p < 0.001$) than during stock growth (period 1978–1989; $y = 291.43 * SSB^{0.3279}$; $r = 0.73$, $p < 0.001$). Interestingly, the same pattern is observed for sardine off California: at larger area per unit biomass during a phase of population decline (period 1951–1963; $y = 923.8 * SSB^{0.4057}$; $r = 0.63$, $p < 0.05$) than during a growth phase (period 1983–2002; $y = 357.9 * SSB^{0.4019}$; $r = 0.86$, $p < 0.001$) (Fig. 8, Table 3). On the other hand, California anchovy appears to show opposite trends to those of sardine: at larger area per SSB unit is occupied during population growth (period 1954–1969, excluding 1986 due to poor survey coverage; $y = 3604.6 * SSB^{0.3341}$; $r = 0.52$, $p < 0.05$) than during population decline (period 1978–1995; $y = 0.0001 * SSB^{1.5735}$; $r = 0.76$, $p < 0.001$) (Fig. 8, Table 3). There is no comparable period of anchovy population decline off Japan to test whether this pattern is consistent between both areas.

4. Discussion

The results presented indicate that the density and distributional area of anchovy and sardine populations off South Africa, Japan, California and Peru, are related to their abundance, generally consistent with the basin model proposed by MacCall (1990) and contrary to the predictions from constant density or proportional models (e.g. Hilborn and Walters, 1992; Petitgas, 1998). This implies that as small pelagic fish populations grow in stock size both
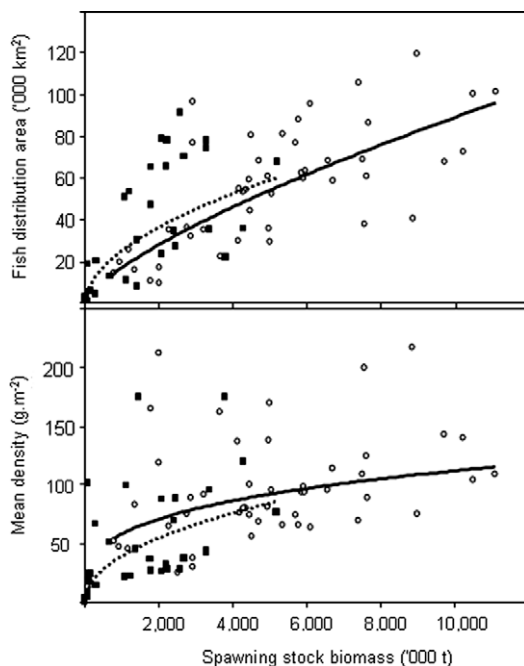

Fig. 8. Relationship between sardine (squares) and anchovy (circles) spawner biomass and spawner area during periods of population growth (solid symbols, solid line) and population decline (open symbols, dotted line). (A) Sardine off Japan, 1990–2004 (decline) and 1978–1989 (growth); (B) California sardine, 1951–1963 (decline) and 1983–2002 (growth); (C) California anchovy, 1978–1995 (decline) and 1954–1969 (growth; 1968 data excluded due to poor survey coverage).

Table 3
Results of the analysis of variance of the regression between area (dependent variable) and biomass (independent variable) for periods of growth and decline (trend) for Japanese sardine, California sardine and California anchovy. Bold values indicate significance at $p < 0.05$. California data refer to CalCOFI datasets (see Section 2).

Region/species parameter		T-statistic	P-value
Japanese sardine	Constant	7.5309	**0.0000**
	Biomass	8.2236	**0.0000**
	Trend	1.7098	0.1008
	Biomass * trend	−4.5322	**0.0001**
	r Adjusted for d.f.	0.92	
California sardine (CalCOFI)	Constant	2.2415	**0.0345**
	Biomass	3.1172	**0.0047**
	Trend	−1.2172	0.2354
	Biomass * trend	−2.416	**0.0237**
	r Adjusted for d.f.	0.74	
California anchovy (CalCOFI)	Constant	−0.2831	0.7796
	Biomass	1.8011	0.0848
	Trend	3.4821	**0.0020**
	Biomass * trend	0.6590	0.5164
	r Adjusted for d.f.	0.83	

Fig. 7. Relationship between anchovy (open circles, solid line) and sardine (closed squares, dotted line) biomass, fish distribution area (top panel) and average packing density (bottom panel), off Peru. Data from surveys 1983–2006 for the region 5–15°S.
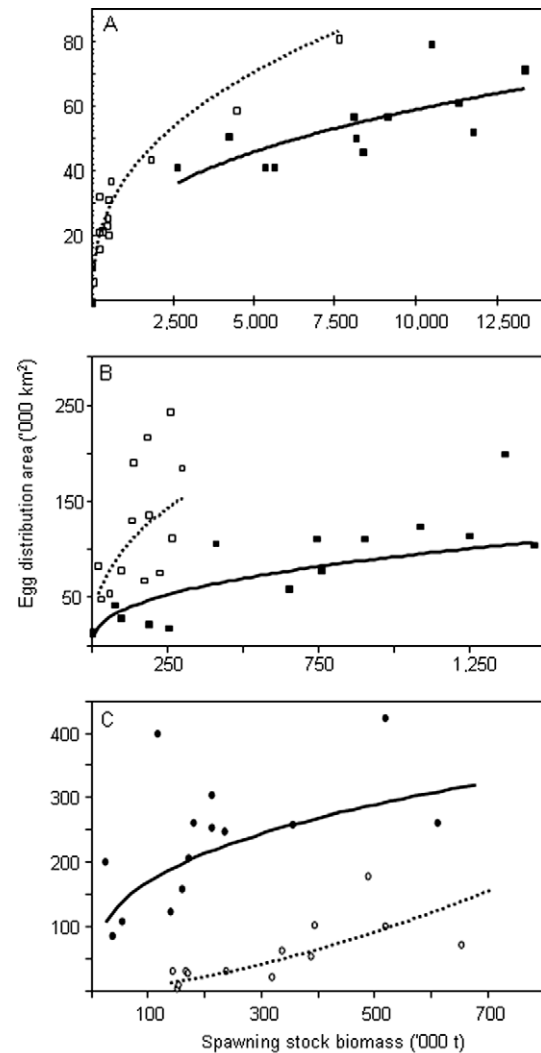
the area they occupy and their packing density increase. The relationship between distribution area and stock biomass is allometric, which implies that there is a limit to the extent of the stock expansion to new areas. As many of the surveys are conducted during the spawning period of one of the two species under investigation, it may be that in these cases the constraint reflects conditions pertinent to spawning only.

Data for California, Japan and Peru, but not for South Africa, also had indications of serial autocorrelation in the residuals (Durbin–Watson test, Table 2). While this does not invalidate the results it indicates a reduced number of degrees of freedom, which needs to be considered when interpreting the correlations. However, it is not believed that this statistical limitation influences the conclusions reached.

Patterns of space occupation appear to differ between sardine and anchovy, consistent with previous work (Barange and Hampton, 1997; Barange et al., 2005; Oozeki et al., 2007). Off South Africa and off Japan anchovy occupies a larger area (adult distribution in the case of South Africa and egg distribution off Japan) per unit biomass than sardine, thus resulting in lower packing densities. This result would be consistent with hypotheses that suggest that population fluctuations may be trophically mediated. Van der Lingen (1994) demonstrated that sardine are mainly filter-feeders off South Africa, whereas anchovy are mainly particle-feeders (zooplankton feeders), thus exploiting a slightly higher trophic level. The inability of anchovy to exploit phytoplankton and microzooplankton as a food source, contrary to sardine, means that anchovy may require a larger distance between individual fish than sardine. It is important to note though that the present analysis is based on fish biomass integrated over a particular time or distance rather than numerical abundance inside schools. An individual sardine would typically be 3–4 times heavier than an anchovy, and this should be factored in before elaborating on any hypothesis that is based on resource use. The difficulty in obtaining length–weight data for all the surveys used, and the use of population densities rather than school densities, precludes further discussion.

Off California and Peru results confirm that in general species also expand their distribution area and increase their packing densities with stock size, but the signal to noise ratio is not as clear as for the previous examples, at least when using the entire time series. It is also difficult to see differences in the patterns between anchovy and sardine. There are several hypotheses that would explain these results. In the case of Peru Bertrand et al. (2008) and Swartzman et al. (2008) argue that the distribution area of anchovy is defined as the area dominated by upwelled waters. Their 'habitat-based' model (Bertrand et al., 2004) indicates that anchovy concentration increases in the favoured habitat when habitat quality increases rather than expanding spatially to less favourable habitats, as the traditional basin model of MacCall (1990) would predict.

The example of California is interesting because the data, despite the different methodologies used in the four regions, indicate much larger distribution area per unit biomass than any other region (Fig. 3). As mentioned earlier, data from South Africa suggests that the distribution of adults may be significantly smaller than that of eggs (Fig. 2), but this factor seems insufficient to explain the differences observed. It may thus be concluded that the factors determining the distribution area of pelagic fish off California may differ from the other regions under study.

Rykaczewski and Checkley (2008) proposed that the production of sardine in the California Current system is related to wind-stress curl, indicating a potential increase in habitat and food supply in the offshore region. In this context it is worth indicating that the trend between biomass and distribution area for California sardine has particularly broken down since 2000, indicating larger distribution area per SSB unit in recent years than expected. Two

hypotheses can be put forward to explain this observation. The first would suggest that excessive exploitation is preventing the stock from re-building its biomass. However, based on the harvest rates estimated in the assessments and the conservative harvest policy in place, this is not very likely to be the case. The second hypothesis would suggest that productivity has declined due to unfavourable conditions for sardine growth (but not distribution). The California Current system is believed to have returned to a cold regime around 1999, with some fundamental change to the system having affected its productivity (Peterson and Schwing, 2003). Cold regimes are known to favour anchovy over sardine (Lluch-Belda et al., 1989, 1992), perhaps explaining production declines. However, according to Rykaczewski and Checkley (2008), curl-driven upwelling would provide extended suitable feeding and spawning habitat for sardine in the offshore region, even if coastal upwelling hinders sustained production in the inshore region.

The lack of clear specific differences in the California dataset may also be because patterns differ between periods of population growth and decline (Fig. 8, see below), as well as differences in survey coverage during the CalCOFI time series. Regarding the latter, if sardine habitat off California expands offshore through jets and filaments, this would not have been reflected in the limited and variable coverage of the CalCOFI survey programme. In this paper we have taken the CalCOFI data as the best available, and have not limited or standardised its coverage to avoid adding more bias to the analysis. However, it is also significant that distribution area calculations are sufficiently reliable so as to have been used in the assessment of California sardine since 1993 (Hill et al., 2007). In conclusion, sampling biases are likely to have influenced the results, possibly masking clearer relationships between biomass and distribution area, but their extent is unclear.

The long-term data series off California and Japan, and the fact that both have experienced at least one cycle of expansion and contraction for either or both species, allows us to explore further the patterns of space use. For sardine, both off California and off Japan, a larger area per unit biomass appears to be required during stock decline than during stock growth (Fig. 6). However, the opposite is observed for anchovy off California. This suggests that while more space is used as the sardine population grows, habitat availability may not be a pre-requisite for this, explaining why sardine packing densities may be larger during initial population growth phases rather than during more stable phases. On the other hand, the results suggest that anchovy may require habitat to become available for populations to grow, implying a dependency on adequate habitat. A differential habitat dependency between both species would again be consistent with their trophic differences. If anchovy need to keep a larger distance between individuals to secure feeding success it may well be that food resources are a limiting factor, thus requiring an increase in the ecosystem's carrying capacity (and thus anchovy habitat) for the stock to grow. Sardine, on the other hand, more able to switch diets depending on availability, may be less specific in its habitat needs. Although this is a simplistic conclusion, the corollary would be that available habitat determines the size of anchovy stocks while the size of sardine stocks may be, on a first level, driven by factors other than habitat availability. Sardine habitat suitability does however play a role. Agostini et al. (2007) used the CalCOFI data set to look at zooplankton abundance characterizing sardine habitat during different phases of their population growth and decline, concluding that access to habitat with decreased predation pressure (from zooplankton on sardine eggs and early stage larvae) during warm years may be a major factor allowing bursts in sardine recruitment. An alternative explanation for the patterns observed is that sardine populations grow in small pockets (requiring less area) while in the case of anchovy it is the whole population that grows in synchrony.

An issue worth discussing is the fact that most surveys, while reporting results for both anchovy and sardine, are specifically targeting one of these species. For example, the acoustic surveys conducted off South Africa are specifically designed according to the distribution and life history of anchovy (Hampton, 1987, 1992; Barange et al., 1999; Barange and Hampton, 1997). While sardine results are used in the assessment and are considered a reliable estimate of the state of the stock (Coetzee et al., 2008a), the design of the survey is not optimised to sardine's life history characteristics (Barange and Hampton, 1997; Barange et al., 2005). Likewise, the spring surveys off California have reasonable coverage of sardine spawning, but less of anchovy, which is known to spawn through the year with peaks from late winter to spring. Because both species have differential cross-shore distribution in most of the regions studied, a survey targeting the species occurring closer to the coast is likely to miss part of the distribution of the offshore species. The most likely consequence of survey inequalities and biases is additional noise, suggesting that the consistent observed patterns of space occupation between species and regions reflect real patterns independent of any data biases. Perhaps the only exception to this statement is the differential biomass versus area relationships during periods of growth and decline between anchovy and sardine off California and Japan. It is possible that the limited number of observations, and the interaction between decadal distribution changes with semi-fixed survey designs, may have biased the results obtained. In this context, the conclusions reached must be taken as hypothetical and requiring further investigation. For example, the relationship between biomass and distribution area off California in the period ~1978–1995 (period of declining anchovy biomass but increasing sardine biomass) appears very similar for both species (solid line in Fig. 8b and dotted line in Fig. 8c), which could reflect a generic decadal pattern of habitat availability at the ecosystem level, rather than species-specific patterns of space occupation (cf. Peterson and Schwing, 2003; Rykaczewski and Checkley, 2008).

Several authors have suggested that anchovy and sardine populations display synchronic out-of-phase abundance fluctuations, indicating that the two species ecologically replace each other to a certain degree. The actual mechanism(s) behind such replacements (and even whether there is replacement, Fréon et al., 2003) remains contentious, involving large-scale atmospheric trends (Chavez et al., 2003), temperature tolerance (Takasuka et al., 2008) and/ or competition for and adaptation to specific food resources (van der Lingen et al., 2006). While each hypothesis has different habitat implications, it is evident that if anchovy and sardine are equivalent species demonstrating synchronic, basin-scale abundance fluctuations, their habitat selection mechanisms should also be similar. In other words, whatever causes one species to decline must act positively on the second species. However, the results presented here suggest that anchovy and sardine cannot be considered to replace each other, as their ecological use of space has significant differences. In the California region, for example, anchovy and sardine overlap in the neritic zone, but at high population levels sardine also occupy vast offshore areas, leaving the inshore region as a nursery ground, while anchovy will remain inshore at all times. No obvious competition for space is observed between anchovy and sardine off Peru (Massé and Gerlotto, 2003) or South Africa (except when the biomass of both species is high, cf. Barange et al., 2005; Coetzee et al., 2008b). This line of thought does not negate the possibility that both species display synchronic fluctuations, but the observations suggest that the major reason for alternation and dominance of one species may be climatic, and not merely behavioural. The ecological mechanisms behind these fluctuations are likely to be much more complex that a simple replacement caused by opposite responses to a given forcing factor.

The specific dependency of small pelagic populations on suitable habitat could be of use to model the potential for species expansion based on habitat mapping predictions. There have been recent attempts to model the worldwide dynamics of anchovy and sardine as driven by climate forcing. Ito et al. (2006) report an effort to link a bioenergetics-based population dynamics fish model (NEMURO.FISH), previously used to examine the responses of Pacific herring (*Clupea pallasii*) and Pacific saury (*Cololabis saira*) to decadal fluctuations in climate, to study the synchrony and asynchrony of sardine and anchovy populations worldwide. The results presented here provide the first comparative, quantitative estimates of biomass/area relationships for pelagic fish, of use in these modeling approaches. Despite the methodological differences, it is worth noting that the habitat required per unit of biomass for species off Japan and South Africa appear to be reasonably comparable, with sardine requiring ~30,000 km² per 100,000 ton of fish and anchovy ~60,000 km² for a similar biomass level. Off Peru fish requires half the area per similar biomass, while off California sardine appears to require 4–5 times the area needed for sardine off Japan and South Africa. This information may provide critical information to understand and predict population responses to climate forcing and change, linking patterns in abundance to patterns with "spatial signatures".

In conclusion, this paper highlights the importance of spatial extent and habitat characteristics to understand population dynamics of fish species. If stock abundance is mediated by spatially explicit processes it seems essential that management tools are designed to account for this.

Acknowledgements

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