



## The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*

Michael Ballón<sup>a,b,\*</sup>, Claudia Wosnitza-Mendo<sup>a</sup>, Renato Guevara-Carrasco<sup>a</sup>, Arnaud Bertrand<sup>a,b</sup>

<sup>a</sup>Instituto del Mar del Perú, Esquina Gamarra y Gral. Valle s/n, Apartado 22, Callao, Lima, Peru

<sup>b</sup>IRD, UR097, CRHMT, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France

### ARTICLE INFO

#### Article history:

Accepted 14 October 2008

Available online 21 October 2008

#### Keywords:

Peruvian hake *Merluccius gayi peruanus*

Fish condition factor

Gonad index

Sex ratio

Overfishing

El Niño southern oscillation

### ABSTRACT

In this study we examine physiological responses of Peruvian hake (*Merluccius gayi peruanus*) to changes in their population structure and physical environment during the period 1971–2004. In particular, we assess the relative investment of energy in growth and/or reproduction of small (20–35 cm) and large (35–50 cm) hake. We calculated the (i) condition (Fulton's K), (ii) gonad and (iii) gut fullness indices for 42,761 female hakes sampled from commercial landings; these indices indicate fish somatic, reproductive and feeding condition, respectively. Using Generalized Additive Models we then examined potential relationships between these indices and sea surface temperature anomalies and date. Drastic energy exhaustion and a decrease in female hake fecundity were observed during El Niño events. The long-term trend showed a general increase in condition factor and a decrease in gonad index for large hake between 1971 and 2004. Small hake exhibited a different trend with an increase in reproductive activity, which was accompanied by an earlier maturation. We hypothesise that the observed low investment of energy in reproduction by large female hake might be related to the lack of large males, due to a sex-selective fishery and the impact of El Niño. We suggest that fishing diminished hake reproductive capacity, modified the sex ratio in favour of females and increased population vulnerability to environmental stress, in particular to the El Niño. The impact of multidecadal variability and predators like the squid, *Dosidicus gigas*, remain unresolved until longer time series become available.

© 2008 Elsevier Ltd. All rights reserved.

### 1. Introduction

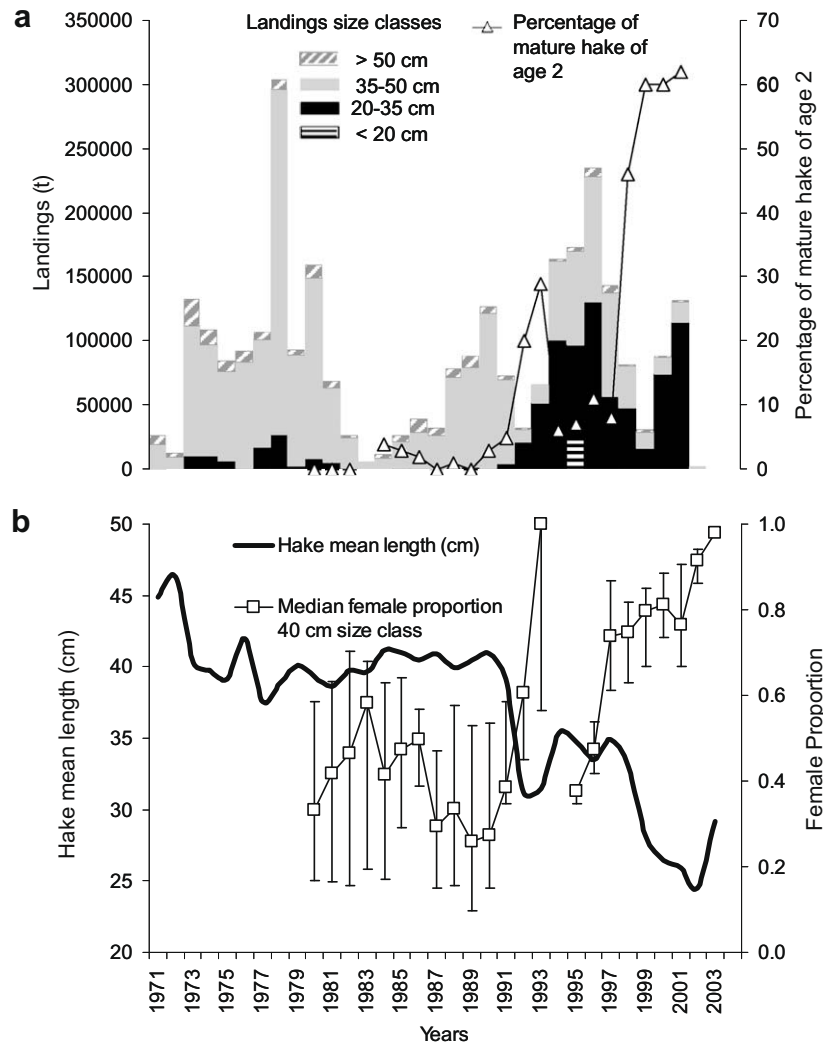
Peruvian hake (*Merluccius gayi peruanus*) is the most abundant commercially exploited demersal fish in the northern Humboldt Current System (Peru). Intense fishing pressure was exerted on hake since the early 1970s. Fishing effort increased from an average of 40 active vessels per year before the 1990s to 74 in the early 2000s (Guevara-Carrasco and Leonart, 2008). It has been hypothesized that fishing caused radical declines in biomass leading to the change of fishery status from fully exploited to overfished and to the closure of the fishery in 2002 (Guevara-Carrasco, 2004). During this period, the population structure changed, exhibiting a drastic reduction in mean hake size (Fig. 1). Large hake (>35 cm) dominated the landings until the late 1980s; after that, smaller hake represented the bulk of the catches. This change was accompanied by an early age of maturation with the percentage of mature hake at the age of 2 years passing from almost zero during the 1980s to more than 60% in the early 2000s (Fig. 1; Wosnitza-Mendo et al., 2004; Guevara-Carrasco and Leonart, 2008). The fishery was reopened after 18

months in 2004 and total allowable catches and individual non-transferable quotas were implemented to control the exploitation of hake. Although there has been a reduction in fishing effort, hake mean size and abundance remain reduced (Guevara-Carrasco and Leonart, 2008).

The Peruvian coast is strongly affected by El Niño that alters the physical (e.g. upwelling efficiency, temperature, salinity, oxygen, vertical stratification), and biological (species composition, abundance, distribution and concentration) environment off Peru (Arntz and Fahrback, 1991; Wolff et al., 2003). El Niño thus affects hake by (i) extending the distribution of hake eggs, larvae (Sandoval de Castillo et al., 1989), juveniles and adults southwards (Samame, 1985), (ii) changing the diet from fish to crustaceans (Sanchez et al., 1985), and (iii) decreasing fishing mortality due to a lower availability (Espino et al., 1985). Many aspects of these changes remain unclear. Indeed, Espino (1990) suggested that El Niño was responsible for the recovery of Peruvian hake population in the 1980s, whereas Wosnitza-Mendo et al. (2004) argued that El Niño was one of the main causes of the decline in hake size during 1991–1992. These opposing views of the possible effects of El Niño on hake (see Espino, 1990; Tam et al., 2006; Wosnitza-Mendo et al., 2004) persist at least partly because of a lack of reliable estimates of natural mortality, making it difficult to separate the effect of the natural environment from that of fishing.

\* Corresponding author. Address: Instituto del Mar del Perú, Esquina Gamarra y Gral. Valle s/n, Apartado 22, Callao, Lima, Peru. Tel.: +56 1 4202000.

E-mail address: [michballon@googlemail.com](mailto:michballon@googlemail.com) (M. Ballón).



**Fig. 1.** (a) Annual hake landings by size classes (histograms), and percentage of mature hake of age 2 (solid line with empty triangles; redraw from Wosnitza-Mendo et al. (2004) and Guevara-Carrasco and Leonart (2008)). (b) Hake mean length in catch over time (smooth black solid line), and median, maximum and minimum hake female proportion in catch for the 37.5–42.5 cm length interval (solid line with empty square).

To determine any overall El Niño effect and to separate it from the long-term effect of fishing we assess the overall condition and reproductive health of hake over time. We assume that El Niño's effect on hake biology can be isolated if an El Niño event provokes a sudden and short term deviation from the long-term trend in hake's condition and reproduction. In this study hake condition and energy investment in reproduction have been assessed using Fulton's condition factor (CF) and gonad index (GI), respectively. Fulton's condition factor indicates the energy budget of the fish (Dutil and Lambert, 1997b), and decreases as a result of starvation (Dutil et al., 2006), investment of energy in reproduction (Lambert and Dutil, 2000), and adverse physical (Takasuka et al., 2005) conditions. The gonad index assesses fish fecundity (Takasuka et al., 2005; Murua et al., 2006). Since fecundity and fish condition are positively correlated (Brooks et al., 1997; Kurita et al., 2003), CF and GI can serve as indices of environmental or feeding conditions (Dutil and Lambert, 1997a). When used in conjunction with fish size data, a compensatory response of small fish to a reduction in overall population size (Trippel, 1995) can be detected.

In this study we calculate the CF, GI and gut Fullness (FI) indices of 42,761 female hake which were sampled between 1971 and 2004, the largest data set ever published on hake. Large and small size classes were assessed to determine if they respond similarly to El Niño and fishing pressure.

We first discuss the effects of El Niño and fishing on CF and GI. Then, long-term trends of fish condition and gonad index are examined with regard to the different responses of large and small hake to a reduction in overall population size and in population size structure, and to the changes in the sex ratio.

## 2. Materials and methods

Hake mean length in catches and catch size structure by size class (<20 cm; 20–35 cm; 35–50 cm; >50 cm) were determined from sampling performed by IMARPE (Ballón et al., 2007). The female proportion of adult hake in catches between 1980 and 2003 was estimated by the Demersal Fish Department of IMARPE. The median of the female proportion in catches, as well as the minimum and maximum proportions of 37.5–42.5 cm long fish were plotted against time to observe their respective trends (Fig. 1).

The hake biological indices were derived from biological sampling of female hake captured by commercial trawlers off Paita (05° S) from 1971 to 2004. Most of the samplings were performed over the whole year (see electronic supplementary material). Total length, body weight, stomach weight, sex and gonad weight were recorded. Fish smaller than 20 cm and larger than 50 cm were excluded because hake smaller than 20 was almost absent from

observations until the mid 1990s and very large hakes were very scarce in samples at the end of the analysed period.

Three indices were calculated for each fish:

1. An indicator of overall health or condition, Fulton's condition factor (CF), with  $W$ ; the total body weight (in g), and  $L$ ; the total length (in cm)

$$CF = W \cdot L^{-3}$$

2. An indicator of reproductive health or condition, the gonad index (GI), with  $Wg$ ; the gonad weight (in g)

$$GI = Wg \cdot W^{-1}, \text{ and}$$

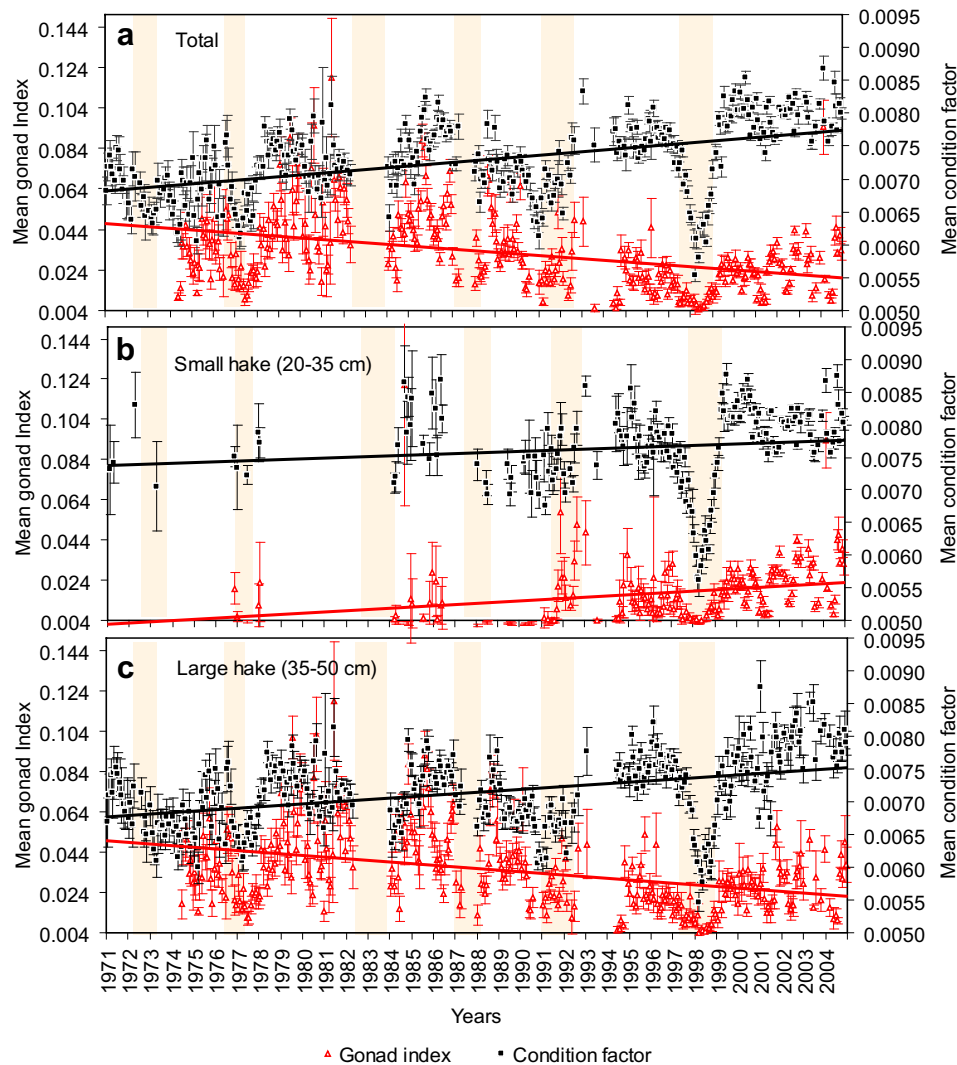
3. An indicator of recent feeding, the fullness index, with  $Ws$ ; the stomach weight (in g)

$$FI = Ws \cdot W^{-1}$$

In addition to the fish indices, monthly anomalies of sea surface temperature (SSTA) at a coastal station in front of Paíta ( $5^{\circ}$  S) were used to assess the physical environment. GI and CF for the entire fish sample and for hake smaller and larger than 35 cm were plotted as monthly averages with their confidence intervals for the

period 1971–2004 (Fig. 2). El Niño periods were also indicated in the same graph to visualize the trends of GI and CF during these periods. Regression lines for each series were adjusted to determine the long-term trend of GI and CF.

We sought potential relationships between CF and the other parameters GI, FI, SSTA and date (year–month) using Generalized Additive Modelling (GAM, Hastie and Tibshirani, 1990); a technique that can detect non-linear and multivariate relationships between variables. Cubic spline smoothing was used to estimate the non-parametric function of CF versus the other parameters using S-Plus (Insightful Corporation, Seattle, WA, USA). Since all sets of variables were incomplete before 1980, the GAMs were constructed for 1980–2004. As hake's diet and relative body, gonad and digestive tract weights are known to depend on fish size (Fuentes et al., 1989; Chouinard and Swain, 2002; Lloret et al., 2002), and because large individuals are known to invest more energy in reproduction than small ones (Scott et al., 2006), fish length was not considered in an overall model. Instead a different model was constructed for each 5 cm fish length interval. Results from a first set of GAM analyses performed by 5 cm fish length interval showed that results were similar for fish size ranging from 20 to 35 cm, and from 35 to 50 cm. For this reason, and to avoid repetitive results, we collapsed the six size classes into two larger classes



**Fig. 2.** Monthly mean condition factor (black full squares)  $\pm$  confidence intervals (black bars), gonad index (red empty triangles)  $\pm$  confidence intervals (red bars) and lineal trends (black and red solid lines) for (a) all sizes, (b) small (<35 cm) and (c) large (>35 cm) female hake from 1971 to 2004. The overlaid areas in salmon colour correspond to El Niño periods.

(20–35 and 35–50 cm), which encompassed and revealed the main trends.

The GAM described above was repeated using the gonad index (GI) as a dependent variable and CF, FI, SSTA and date as independent variables. Although the relationship between CF and GI was evaluated in the first GAM, it was examined again with GI as the dependent variable, in order to provide the complete matrix of independent variables for each GAM.

### 3. Results

#### 3.1. Hake size structure and female proportion in catches

Hake size structure in landings showed drastic changes between 1971 and 2003. During this period, hake mean size decreased from over 40 cm to about 25 cm (Fig. 1b). Hake landings were dominated by fish larger than 35 cm during the 1970s–1980s, then by hake smaller than 35 cm. In recent years, hakes larger than 35 cm represented a very small proportion of the catches (Fig. 1a). These changes in size structure coincided with (i) an increase in the female proportion in catches from about 40% at the beginning of 1990 to almost 100% at the beginning of 2000 (Fig. 1b; for more details on changes in sex ratio, see Guevara-Carrasco and Leonart, 2008), and (ii) an increase in the percentage of mature hake of age 2 from almost zero to about 60% in the early 2000s (Fig. 1a).

#### 3.2. Time series of condition factor versus gonad index

Time series of Fulton's condition factor (CF), gonad index (GI) for all hake showed different trends depending on the time period (Fig. 2a). CF was positively correlated with time ( $p < 0.05$ ) whereas GI was negatively correlated with time ( $p < 0.05$ ). However, it is important to note that the range of hake length has not been constant over time. Samples were dominated by large hakes during the first two decades and by small hakes during the last decades (Fig. 1a), and GI values have been low since the early 1990s. These overall results are similar to those obtained for large hake (35–50 cm) (Fig. 2c). Results for small hake (20–35 cm) are different (Fig. 2b), because both CF and GI increased according to time even if these trends were not statistically significant ( $p > 0.05$ ). Over shorter periods, CF and GI vary in phase, in particular during El Niño events, which had a strong negative effect on both parameters, whatever the size class considered (Fig. 2).

#### 3.3. Generalized additive models

GAM results show that GI, FI, SSTA and time explained 32% and 27% of the deviance of CF for the large and small size classes, respectively. The four tested variables each had significant effects (Table 1). The relationships between CF and the biological indices GI and FI were linear and positive for both size classes (Fig. 3a and b), i.e., large GI and FI values predicted a high CF. The SSTA had negative effects on the CF for both large and small hake (Fig. 3c): positive SSTA, corresponding to El Niño, coincided with reduced CFs for both size classes. To a lesser extent, negative anomalies associated with La Niña might reduce CF. The highest CFs for both size classes occurred with small positive temperature anomalies ( $\sim 0.3^\circ\text{C}$ ). The trend in CF for large hake (Fig. 3d) was similar to that for all hake, with low CF values during the 1980s which increased from the early 1990s. CF for small hake decreased during the 1980s, increased during the 1990s, and then decreased again after 2000 (Fig. 3d).

GAM analysis of gonad index versus CF, FI, SSTA and date explained 28% and 12% of the deviance of the GI for large and small

**Table 1**

Statistical characteristics of GAMs based on Fulton's condition factor (CF) and gonad index (GI) for the small (<35 cm) and large hake (>35 cm).

Variable	Source	d.f.	P	Resid. d.f.	Residual deviance	% Explained
<i>Small hake (20–35 cm)</i>						
CF	NULL			21,699	0.0164	
	GI	1	0.00004	21,698	0.0150	8.70
	FI	1	0.00000	21,697	0.0138	6.87
	SSTA	1	0.00000	21,696	0.0130	5.00
	Time	13	0.00000	21,683	0.0120	6.44
	Model			21,683	0.0120	27.01
GI	NULL			21,699	14.2039	
	CF	1	0.00000	21,698	12.9676	8.70
	FI	1	0.00037	21,697	12.9047	0.44
	SSTA	1	0.00000	21,696	12.9012	0.02
	Time	13	0.00000	21,683	12.5235	2.66
	Model			21,683	12.5235	11.83
<i>Large hake (35–50 cm)</i>						
CF	NULL			15,168	0.0118	
	GI	1	0.00000	15,167	0.0110	6.59
	FI	1	0.00000	15,166	0.0100	9.03
	SSTA	1	0.00000	15,165	0.0097	1.85
	Time	13	0.00000	15,152	0.0080	14.56
	Model			15,152	0.0080	32.03
GI	NULL			15,168	16.2778	
	CF	1	0.00000	15,167	15.2059	6.59
	FI	1	0.00000	15,166	14.6550	3.38
	SSTA	1	0.00000	15,165	14.6140	0.25
	Time	13	0.00000	15,152	11.7009	17.90
	Model			15,152	11.7009	28.12

hake, respectively. Significant effects were found for all independent variables (Table 1). Date had a positive effect on GI for small hakes and a negative effect on GI for large hakes. Fish CF had a positive effect on GI whatever the size, while FI negatively affected GI (Fig. 4). As for CF, the lowest GI values for both size classes (Fig. 4c) were related to large positive El Niño-related SSTA. The relation between SSTA and maximum GI varied according to fish size; it was  $1^\circ\text{C}$  for large hake and close to  $0.3^\circ\text{C}$  for small ones (Fig. 4c). GI variations over time for the two size classes (Fig. 4d) differed. Large hake had a high GI at the beginning of the 1980s which decreased during the mid 1990s and has remained low. Small hake showed a slow increase in GI from the 1980s through 2000; GI then increased more rapidly (Fig. 4d).

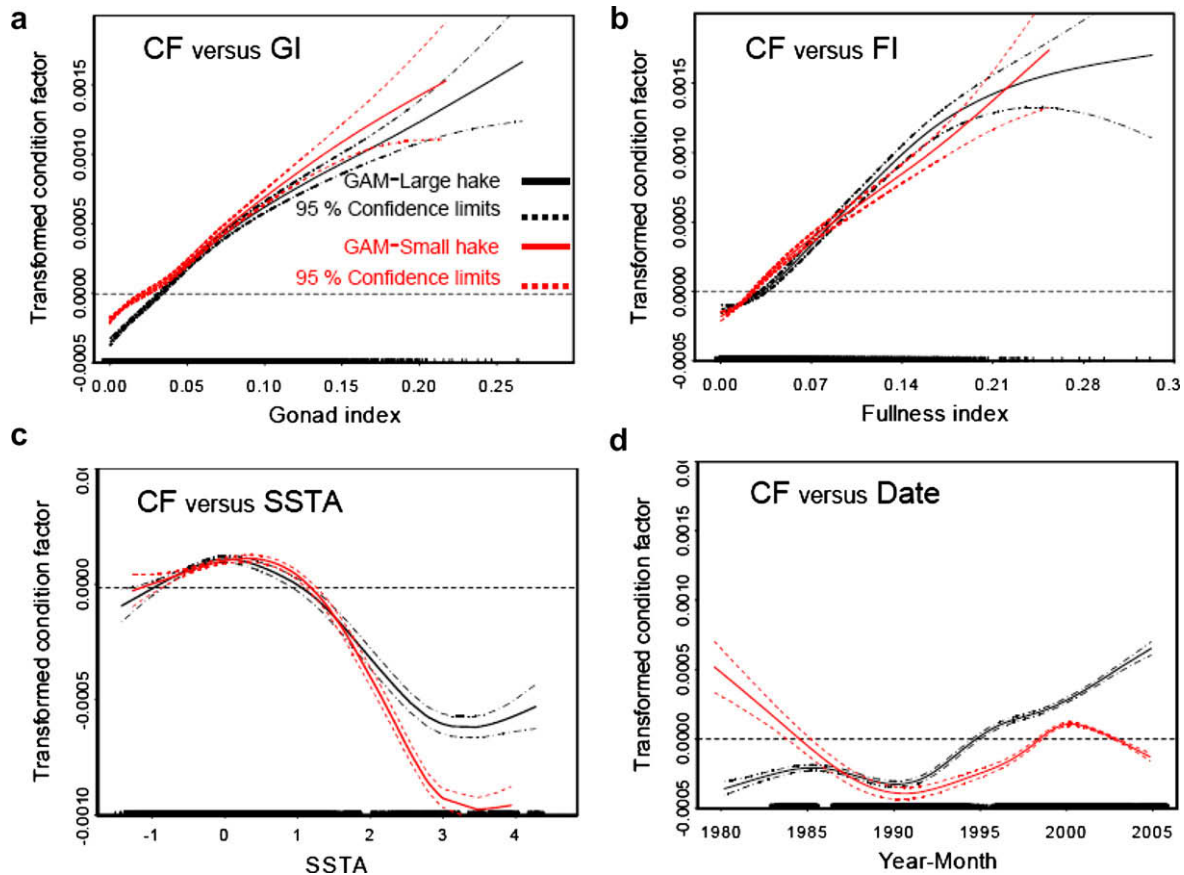
## 4. Discussion

#### 4.1. Reproduction, starvation and El Niño

Fish in good condition (high CF) had large gonads (high GI), but fish with large gonads had nearly empty stomachs (FI; Figs. 3 and 4). This result suggests that the amount of energy devoted to reproduction depends on overall fish condition, and further suggests that hake with the largest gonads do not feed actively or well. The slope of these relationships was steeper for large hake than small hake, which might be the result of a lower proportion of immature fish in the large size class in comparison to the small size class (Fig. 1a). This indicates that, on average, large hake invests more energy in reproduction and feeds less than small hake, suggesting a higher sensitivity to environmental perturbation (e.g. El Niño) than small hake.

Hake distribution is restricted by the presence of the oxygen minimum zone. During El Niño, the oxygen concentration near the bottom increases, expanding hake's range of distribution and favouring the development of new macrobenthic production (Gutiérrez et al., 2008), in particular the crustaceans that account for a large part of hake diet during El Niño (Tam et al., 2006). Un-





**Fig. 3.** Cubic spline fits (solid lines) of GAMs based on Fulton's condition factor (CF) according to: Gonad index (a), fullness index (b), sea surface temperature anomaly (c) and date (d) for large (black lines) and small (red lines) hakes. Each panel shows the kind of relationship that exists between the transformed condition factor (y-axes) and the x variable (x-axes). The transformed condition factors are in relative scale and they correspond to the spline smoother that was fitted on the data so that a y-value of zero is the mean effect of the x variable on the transformed condition factor. Positive and negative y-values indicate positive and negative effect respectively on the transformed condition factor. The dotted lines show the 95% confidence limits of GAMs.

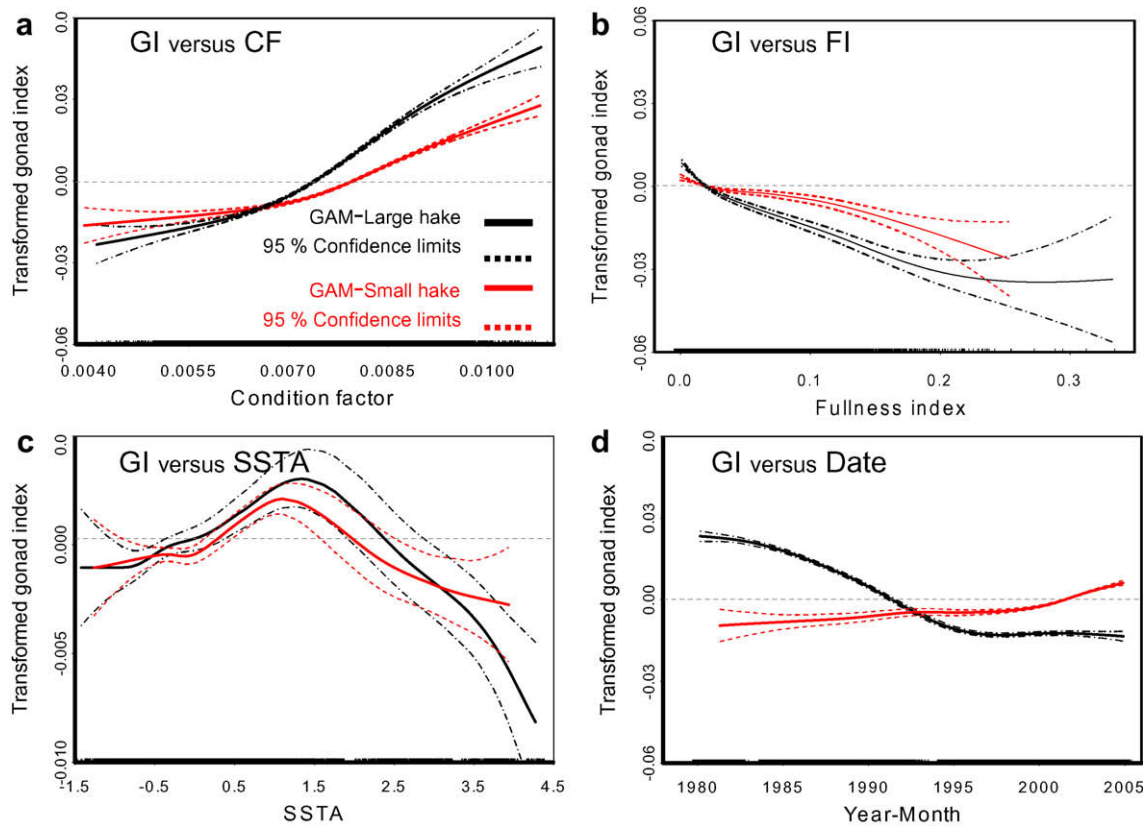
der El Niño conditions, apparently favourable, hake condition and reproduction output should improve. However, we observed that El Niño has a strong negative effect on hake biology (depressed CF and GI; Figs. 2–4). The low GI and CF observed during El Niño contradict the idea that these events favour hake (Espino, 1990). Additionally, low hake CFs during El Niño suggest that hake feeding was affected during these events and challenge the idea that hake fully compensates for the lack of small pelagic fish by feeding on alternate prey, for instance by feeding more on crustaceans than fish (Sanchez et al., 1985; Tam et al., 2006). Even if hake adapts foraging during El Niño, the overall effect on CF is negative. Studies on Atlantic cod (*Gadus morhua*) highlighted that extreme environmental conditions, in which food is scarce for a long period, reduce condition factor and reproductive output (Dutil et al., 1999; Dutil and Brander, 2003). A very low condition of adult fish is also associated with a reduction in fecundity (Lambert and Dutil, 2000) and an increase in adult mortality due to reproduction (Dutil and Lambert, 2000). Indeed, reproduction investment could be maintained (even if lower than during favourable periods) at the expense of somatic condition, in which case, the risk of mortality due to exhaustion of energy reserves would increase (Lambert and Dutil, 2000). If hake reproduction took place during or immediately after El Niño, when hake condition and fecundity were minimum and more severe for large hake (Figs. 2–4), mortality and a decrease in recruitment success would likely occur. In any case, El Niño represents a strong environmental stress.

#### 4.2. Overfishing

Overfishing primarily affects large fish (e.g. Pauly et al., 1998) and can aggravate the low abundance periods due to natural variability. If fish concentrate to keep certain density levels in order to form functional spatial aggregation (i.e., for schooling, mating, spawning), a fishery can continue to exploit fish patches even at a low stock level (Rose and Kulka, 1999). Consequently, both mean fish size and distribution area decrease. Indeed, high predation (or fishing) pressure increases the risk of a population collapse (Shoener et al., 2001). This seems to apply to Peruvian hake as intense fishing depleted the population, especially the adult proportion (Fig. 1), and reduced its area of distribution (Guevara-Carrasco and Leonart, 2008). The probable higher vulnerability of large hake to fishing and to El Niño combined with its depleted population and diminished distribution area could explain the disappearance of adults during and following the El Niños of 1991–1992 and 1997–1998 (Wosnitza-Mendo et al., 2004).

#### 4.3. Long-term changes

The overall trend shows that CF increased and that GI decreased from 1971 to 2005 (Fig. 2a). This trend was observed for large fish but not for small hake (Figs. 2–4). Small hake's reproductive activity increased over time, especially during the last years (Fig. 4), and was accompanied by a decrease in condition factor. A high proportion of immature fish composed the small size class during the



**Fig. 4.** Cubic spline fits (solid lines) of GAMs based on gonad index (GI) according to: Fulton condition factor (a), fullness index (b), sea surface temperature anomaly (c) and date (d) for large (black lines) and small (red lines) hakes. Each panel shows the kind of relationship that exists between the transformed gonad index ( $y$ -axes) and the  $x$  variable ( $x$ -axes). The transformed gonad indices are in relative scale and they correspond to the spline smoother that was fitted on the data so that a  $y$ -value of zero is the mean effect of the  $x$  variable on the transformed gonad index. Positive and negative  $y$ -values indicate positive and negative effect respectively on the transformed gonad index. The dotted lines show the 95% confidence limits of GAMs.

early years, and it has substantially reduced in the last years (Fig. 1a; Wosnitza-Mendo et al., 2004; Guevara-Carrasco and Leonart, 2008). The observed opposite trends of GI and CF suggest that an immature fish reaches a higher CF than a mature fish of similar size. Why did small hake invest relatively more in reproduction than large hake, even with low CFs?

When population biomass is high and close to the carrying capacity, food limitation can lead to a reduction in reproductive output (Hilborn and Walters, 1992). The hake population, however, has been at a low level since the late 1990s (Guevara-Carrasco and Leonart, 2008) and has exhibited high CFs. Smaller size at maturity (Fig. 1; Wosnitza-Mendo et al., 2004; Guevara-Carrasco and Leonart, 2008) could compensate for the lack of large adults. Some fish can mature at a smaller size if well-nourished (Trippel, 1995). It is also possible that fishing produces evolutionary pressure for a reduction in size at first maturity (Conover and Munch, 2002; Reznick and Ghalambor, 2005; Swain et al., 2007). These processes may explain the increasing reproductive activity observed in small hake during the last years. They do not, however, explain the still-perplexing low investment in reproduction by those large hakes that have been sampled.

Long term environmental oscillation of the oceanographic condition could have also influenced the CFs and GIs of small and large hake. Warm-to-cool regime shifts have occurred throughout the eastern Pacific during the late 1980s early 1990s and coincide with the changes in the population of several marine organisms (e.g. Chavez et al., 2003; Alheit and Niquen, 2004; Gutiérrez et al., 2007). A change in the trends of CFs and GIs for large and small hake also occurred at the beginning of the 1990s (Figs. 3 and 4d),

when the last decadal cooling began ('La Vieja' conditions, see Chavez et al., 2003). However, the change in the trends is not 'consistent' (e.g. U-shape for small hake CF, Fig. 3d) indicating that decadal variation is probably not the main effect observed in our data. Furthermore, in this study, neither CF nor GI have been strongly affected by negative SSTA (Figs. 3 and 4c).

Another environmental factor that has not been considered in this study is the expansion of the jumbo squid (*Dosidicus gigas*), a potential predator for hake, whose biomass increased dramatically during the 1990s off Peru (Taípe et al., 2001). Indeed, off western North America, the expansion of the jumbo squid population coincided with the decline in abundance of the Pacific hake (*Merluccius productus*) (Zeidberg and Robison, 2007), which is the main prey of the jumbo squid over the shelf and slope in this region (Field et al., 2007). However, the evidence for high predation of jumbo squid on the Peruvian hake is inconclusive (Tam et al., 2008). Taylor et al. (2008), in a modelling study, concluded that predation from jumbo squid did not influence the trend in hake abundance. There is a need for further studies to determine if jumbo squid has impacted the Peruvian hake population.

Large fish have higher fecundity (Takasuka et al., 2005; Murua et al., 2006), better egg quality and higher egg viability than small fish (Brooks et al., 1997). For instance, larger Atlantic cod have much higher fecundity and hatching rates than smaller fish (Trippel, 1998). Large individuals contribute disproportionately to the reproductive potential of a stock (i.e. Argentinean hake, *Merluccius hubbsi*; Macchi et al., 2004). Mean length in landings of Peruvian hake decreased from around 40 cm during the 1970s and 1980s to 25 cm in early 2000s (Fig. 1). Thus, the rarity of large female

Peruvian hake and their low GIs since the late 1990s likely indicate diminished reproductive capacity.

#### 4.4. Reproductive failure: a male affair?

Females need males to reproduce, but it has always been assumed that female reproduction does not depend on the number and/or the size of males. Studies on the reproductive behaviour of Atlantic cod (Morgan and Trippel, 1996) and Argentinean hake (Pájaro et al., 2005) have shown that males arrive first, are in higher proportion in the spawning areas and stay longer than females. Females enter the area when ready to spawn and leave it after. This behaviour could make males more vulnerable to fishing. If so, exploitation can alter the sex ratio and potentially reduce the probability that females will encounter mates (Moller and Legendre, 2001).

Trawl data (Paita harbour, 05° S) show that male hake accounted for the majority of the catch early in the fishery. The proportion of females in catch increased from about 40% during the 1980s and early 1990s to 80% in the late 1990s and almost 100% in the early 2000s (Fig. 1; Guevara-Carrasco and Leonart, 2008). This lack of males could lead to sperm limitation (Rankin and Kokko, 2006). Perhaps more importantly, the shortage of sperm or male pheromone could inhibit females from spawning (Rideout et al., 2005). According to Rowe and Hutchings (2003), individuals unable to gain access to mates might benefit by reallocating energetic resources from reproduction to growth, which might improve reproductive success in subsequent years. We assume that this is the case for large female Peruvian hake, which exhibited high CFs and low GIs when large males were scarce.

We suggest that fishing has diminished hake's reproductive capacity, has modified the sex ratio in favour of females, increased population vulnerability to environmental stress, in particular El Niño, and has lowered population resilience to such an extent that hake population recovery could take longer or even fail altogether if the increase in stock spawning biomass alone (based on a reduction in fishing effort) is to be the main indicator of recovery.

#### Acknowledgements

The authors gratefully thank the Instituto del Mar del Perú (IMARPE) for having facilitated the use of the data. This work is a contribution of the INCOFISH project (Integrating Multiple Demands on Coastal Zones with Emphasis on Fisheries and Aquatic Ecosystems, of the European Commission, Contract Number 003739) and of the Research Unit 'Upwelling Ecosystems' UR 097 from IRD. We warmly thank Tim Pennington for the English edition and valuable comments on the first version of the MS. We also thank Johanna Holmgren for proofreading many versions of the MS. Finally we thank the anonymous referees for their very helpful comments and suggestions.

#### References

Arntz, W., Fahrbach, E., 1991. El Niño – Klimaexperiment der Natur: physikalische Ursachen und biologische Folgen. Birkhauser, Basel, Boston, Berlin.

Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* 60, 201–222.

Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., Benites, C., 2007. Shifting baseline of demersal species in the Humboldt current system. In: Nicholls, J.H., (comp) Incofish Project Database (<<http://www.incofish.org>>).

Brooks, S., Tyler, C., Sumpter, J., 1997. Egg quality in fish: what makes a good egg? *Reviews in Fish Biology and Fisheries* 7, 387–416.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221.

Conover, D., Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297, 94–96.

Chouinard, G.A., Swain, D.P., 2002. Depth-dependent variation in condition and length-at-age of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 1451–1459.

Dutil, J.D., Brander, K., 2003. Comparing productivity of North Atlantic cod stocks and limits to growth production. *Fisheries Oceanography* 12, 502–512.

Dutil, J.D., Castonguay, M., Gilbert, D., Gascon, V., 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 56, 1818–1831.

Dutil, J.D., Godbout, G., Blier, P.U., Groman, D., 2006. The effect of energetic condition on growth dynamics and health of Atlantic cod (*Gadus morhua*). *Journal of Applied Ichthyology* 22, 138–144.

Dutil, J.D., Lambert, Y., 1997a. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences* 54, 104–112.

Dutil, J.D., Lambert, Y., 1997b. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 2388–2400.

Dutil, J.D., Lambert, Y., 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 57, 826–836.

Espino, M., 1990. El Niño su impacto sobre los peces demersales del Perú. *Boletín Instituto del Mar del Perú* 14 (2), 3–10.

Espino, M., Maldonado, M., Benites, C., 1985. Situación de la Población de Merluza (*Merluccius gayi peruanus*) durante El Niño. In: Arntz, W., Landa, A., Tarazona, J. (Eds.), *El Niño Su Impacto en la Fauna Marina*. Boletín Instituto del Mar del Perú-Callao Volumen Extraordinario, pp. 159–162.

Field, J.C., Baltz, K., Phillips, A.J., Walker, W.A., 2007. Range expansion and trophic interactions of the jumbo squid, *Dicodicus gigas* in the California current. *California Cooperative Oceanic Fisheries Investigation Reports* 48, 131–146.

Fuentes, F., Antonietti, E., Muck, P., 1989. Alimentación de la merluza (*Merluccius gayi peruanus*) de la zona de Paita. In: Jordán, R., Kelly, R., Mora, O., Vildoso, A., de, Ch., Henríquez, N. (Eds.), *Memorias del simposio internacional de los recursos vivos y las pesquerías en el Pacífico Sudeste 9–13 de mayo 1988*. Viña del Mar, Chile. CPPS, Revista Pacífico Sur (Número Especial), pp. 276–289.

Guevara-Carrasco, R., 2004. Peruvian hake overfishing: misunderstood lessons. *Boletín Instituto del Mar del Perú* 21, 27–32.

Guevara-Carrasco, R., Leonart, J., 2008. Dynamics and Fishery of the Peruvian hake: between the nature and the man. *Journal of Marine Systems* 71, 249–259.

Gutiérrez, D., Enríquez, E., Purca, S., Quipúzcoa, L., Marquina, R., Flores, G., Graco, M., 2008. Remotely – driven temporal variations of the subsurface dissolved oxygen content and responses of the continental shelf benthic subsystem off Central Peru. *Progress in Oceanography* 79, 177–189.

Gutiérrez, M., Swartzman, G., Bertrand, A., Bertrand, S., 2007. Anchovy and sardine spatial dynamics and aggregation patterns in the Humboldt Current ecosystem Peru from 1983–2003. *Fisheries Oceanography* 16, 155–168.

Hastie, T., Tibshirani, R., 1990. *Generalized Additive Models*. Chapman and Hall, London.

Hilborn, R., Walters, C., 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, New York.

Kurita, Y., Meier, S., Kjesbu, O.S., 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *Journal of Sea Research* 49, 203–219.

Lambert, Y., Dutil, J.-D., 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 815–825.

Lloret, J., Gil de Sola, L., Souplet, A., Galzin, R., 2002. Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science* 59, 1215–1227.

Macchi, G.J., Pajaro, M., Ehrlich, M., 2004. Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research* 67, 25–38.

Moller, A.P., Legendre, S., 2001. Allee effect, sexual selection and demographic stochasticity. *Oikos* 92, 27–34.

Morgan, M.J., Trippel, E.A., 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science* 53, 820–826.

Murua, H., Lucio, P., Santurtun, M., Motos, L., 2006. Seasonal variation in egg production and batch fecundity of European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *Journal of Fish Biology* 69, 1304–1316.

Pájaro, M., Macchi, G.J., Martos, P., 2005. Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research* 72, 97–108.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down the marine food webs. *Science* 279, 860–863.

Rankin, D.J., Kokko, V., 2006. Do males matter? The role of males in population dynamics. *Oikos* 116 (2), 335–348.

Reznick, D., Ghalambor, C., 2005. Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 62, 791–801.

Rideout, R., Rose, G., Burton, M., 2005. Skipped spawning in female iteroparous fishes. *Fish and Fisheries* 6, 50–72.

- Rose, G.A., Kulka, D.W., 1999. Hyperaggregation of fish and fisheries: how catch per unit effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences* 56, 118–127.
- Rowe, S., Hutchings, J.A., 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* 18, 567–572.
- Samamé, M., Castillo, J., Mendieta, A., 1985. Situación de las pesquerías Demersales y los Cambios durante El Niño. In: Arntz, W., Landa y, A., Tarazona, J. (Eds.), *El Niño su impacto en la fauna marina*. Boletín Instituto del Mar del Perú. Extraordinario, pp. 153–158.
- Sanchez, G., Alamo, A., Fuentes, F., 1985. Alteraciones de la dieta alimentaria de algunos peces comerciales por efecto del fenómeno El Niño. In: Arntz, W., Landay, A., Tarazona, J. (Eds.), *El Niño su impacto en la fauna marina*. Boletín Instituto del Mar del Perú. Extraordinario, pp. 135–142.
- Sandoval de Castillo, O., Wosnitza-Mendo, C., Muck, P., Carrasco, S., 1989. Abundance of hake larvae and its relationship to hake and anchoveta biomasses off Perú. In: Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. ICLARM Conference Proceedings 18, pp. 280–296.
- Scott, B.E., Marteinsdottir, G., Begg, G., Wright, P., Sigurd Kjesbu, O., 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling* 191, 383–415.
- Shoener, T., Spiller, D., Losos, J., 2001. Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412, 183–185.
- Swain, D., Sinclair, A., Hanson, J., 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B* 274, 1–8.
- Taibe, A., Yamashiro, C., Mariategui, L., Rojas, P., Roque, C., 2001. Distribution and concentration of jumbo flying squid (*Dosidicus gigas*) off the Peruvian coast between 1991 and 1999. *Fisheries Research* 54, 21–32.
- Takasuka, A., Oozeki, Y., Kubota, H., Tsuruta, Y., Funamoto, T., 2005. Temperature impacts on reproductive parameters for Japanese anchovy: comparison between inshore and offshore waters. *Fisheries Research* 76, 475–482.
- Tam, J., Purca, S., Duarte, L.O., Blaskovic, V., Espinoza, P., 2006. Changes in the diet of hake associated with El Niño 1997–1998 in the northern Humboldt Current ecosystem. *Advances in Geosciences* 6, 63–67.
- Tam, J., Taylor, M.H., Blaskovic, V., Espinoza, P., Ballón, R.M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N., Wolff, M., 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions. *Progress in Oceanography* 79, 352–365.
- Taylor, M.H., Tam, J., Blaskovic, V., Espinoza, P., Ballón, R.M., Wosnitza-Mendo, C., Argüelles, J., Díaz, E., Purca, S., Ochoa, N., Ayón, P., Goya, E., Quipuzcoa, L., Gutiérrez, D., Wolff, M., 2008. Trophic flows in the Northern Humboldt Current Ecosystem, Part 2: Elucidating mechanisms of ecosystem change over an ENSO cycle by simulating changes in low trophic level dynamics. *Progress in Oceanography* 79, 366–378.
- Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. *Bioscience* 45, 759–771.
- Trippel, E.A., 1998. Egg size and viability and seasonal offspring production of young Atlantic Cod. *Transactions of the American Fisheries Society* 127, 339–359.
- Wolff, M., Wosnitza-Mendo, C., Mendo, J., 2003. The Humboldt Current trends in exploitation protection and research. In: Hempel, G., Sherman, K. (Eds.), *Large Marine Ecosystems of the world*. Elsevier B.V..
- Wosnitza-Mendo, C., Guevara-Carrasco, R., Ballón, M., 2004. Possible causes of the drastic decline in mean length of Peruvian hake in 1992, vol. 21. *Boletín Instituto del Mar del Perú*. pp. 1–26.
- Zeidberg, L.D., Robison, B.H., 2007. Invasive range expansion by the Humboldt squid *Dosidicus gigas* in the eastern North Pacific. *Proceedings of the National Academy of Sciences* 104, 12948–12950.