Adaptive Response of Peruvian Hake to Overfishing

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Abstract

Compensatory mechanisms of the Peruvian hake population (*Merluccius gayi peruanus*) in response to heavy exploitation and changes in species interaction are discussed. Changes in the rate of cannibalism, diet composition, maximization of fecundity and behavioral adaptation are noted.

History of the Fishery

Peruvian hake, a demersal species, is normally distributed on the shelf and the upper part of the continental slope off Peru (from around 3°S to 10°S). Hake is the most important species in Peruvian bottom trawl fisheries. It has been harvested on a commercial scale since the 1960s, initially by a local fleet of small trawlers with less than 100 gross registered tons (GRT) and annual landings of less than 20 000 t. Since the 1970s, foreign fleets with large factory trawlers up to 2 000 GRT have entered the fisheries, increasing annual landings to more than 100 000 t, with a record landing of about 300 000 t in 1978 (Fig. 1).

In the early 1980s, Peruvian hake was already under intensive fishing pressure. The occurrence of "El Niño Southern Oscillation" (ENSO) in 1982-1983, however, produced a change in the distribution and concentration of the population and restricted the normal action of the fleet. Only the local fleet continued fishing until the end of the decade, yielding annual landings of about 20 000 t. During a short period between the end of the 1980s and the early 1990s, hake was harvested by a fleet of midwater trawlers as by-catch in horse mackerel (*Trachurus picturatus*) fishing. The landings increased to about 130 000 t, generated by higher fishing pressure. This new phase of high landings was interrupted by a new ENSO event in 1991-1993. After 1994 landings increased, reaching 200 000 t in 1996. Fishing effort increased significantly with the entry of medium-sized trawlers with advanced technology. Again the ENSO of 1997-1998 caused changes in the distribution and concentration of the population and reduced fishing activities. Landings were only 75 500 t in 1998.

In 1992, a significant reduction in the mean length of catch was observed, from 38-40 cm to 30-33 cm (male-female). After a slight recuperation in 1994, there has been a persistent decline (Fig. 2) suggesting growth overfishing. Evaluation of the biomass estimates from demersal trawl surveys and cohort analyses over the last few years also show a decline to about half the biomass values of the 1980s. Nevertheless, catches in the last eight years have increased constantly (except 1998 and 1999), with about 43-90% of fishes below the length at first maturity (35 cm).

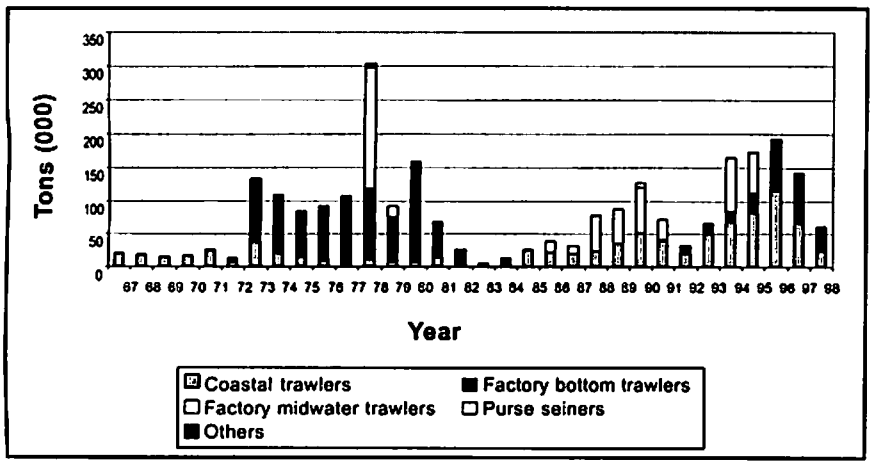

Fig. 1. Landings of Peruvian hake.

Life History Strategies

If we consider ecological theory on r versus K selection, it has proved to be a good tool for classifying different extremes in life history strategy. The parameters of the intrinsic rate of increase in population size (r) and carrying capacity of the environment (K) from the logistic population growth model [dN/dt=rN((K-N)/K)] are presumably determined by natural selection in different species. At one extreme, r-strategists tend to colonize highly fluctuating habitats so

that natural selection will favor a short generation time and use available energy for reproduction. They are normally small in size. In contrast, K-strategists live in habitats with more or less stable mortality factors so that natural selection will favor a longer generation time and use energy to increase survival through different mechanisms. K-strategists seldom deviate from long-term equilibrium situations (Gunderson 1980).

A spectrum of life history types between these extremes exists in nature. In the Peruvian upwelling system, hake is supposed to be more of a K-strategist. But if a population is reduced far below the carrying capacity, the optimum strategy is no longer to minimize the reproductive effort but rather to increase productivity (Estes 1979). Thus a change towards r-strategy seems to have occurred in Peruvian hake in the 1990s. This could be part of the explanation for the resilience of Peruvian hake even under heavy fishing pressure over the last few years.

Resilience of the Peruvian Hake

Alheit and Pitcher (1995b) suggest that cannibalism and ambush predation might be two of the most important biological factors in the resilience of the Peruvian hake. The authors suggest several compensatory mechanisms that account for the differences between the 1980s and the 1990s. The distribution of the Peruvian hake is closely related to the Cromwell Current, branches of which flow north-south between 100-500 m depth and which changes its southward extension depending on summer/winter conditions. It is also related to the occurrence of ENSO. Hence, the area inhabited by the Peruvian hake changes constantly and the extended area during ENSO favors the population, mainly by reduced availability and reduced cannibalism (Espino and Wosnitza-Mendo 1988). Cannibalism has been estimated at about 30% of the natural mortality rate, depending on age, season and year (Castillo et al. 1989).

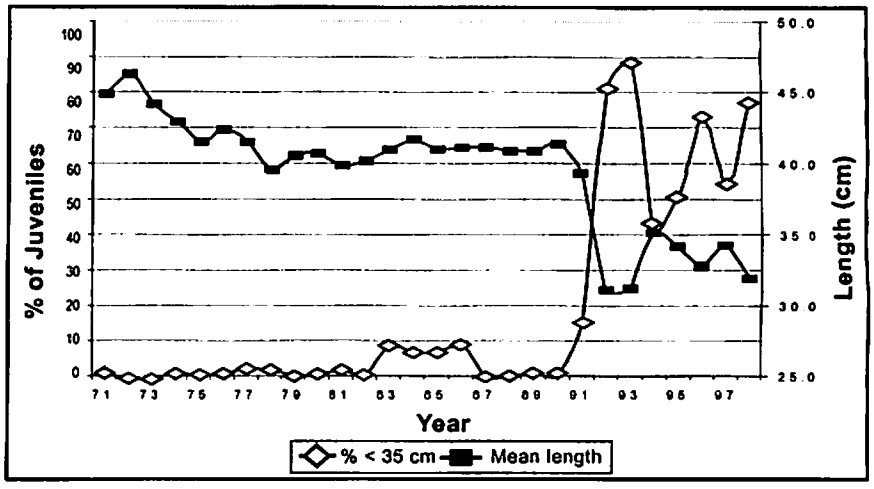

Fig. 2. Mean length and juvenile by-catch of Peruvian hake.

Cannibalism

Looking at cannibalism from an evolutionary aspect suggests that feeding on conspecies presents a diet of high nutritional quality for maximum growth (Smith and Reay 1991). Lifetime reproductive success might also be enhanced by cannibalism. Cannibalism seems to be a strategy that increases an individual's contribution of genes to the next generation through improved survival and reproduction success.

In the 1980s cannibalism ranked fourth in the food spectrum of adult Peruvian hake. In 1980, only 2.3% of the total weight of the stomach content, occupying rank 8, consisted of hake (Fuentes et al. 1989). Due to the absence of sardines (*Sardinops sagax sagax*) and bereche (*Ctenosciaena peruviana*) in the 1990s, this pattern changed and hake itself took the first rank as food item in samples from the winter cruises of 1994, 1995, 1996 (80% in weight of total stomach content in an extremely cold year), 1997 (49% in weight of total stomach content in warm El Niño year) and 1998 (about 53%).

The average length of predator hake also changed. In the 1980s only hake greater than 45 cm were cannibals. In the 1999 demersal bottom cruise, hake of 12-15 cm were found with up to 20 hake prey individuals of about 4-5 cm. Thus, in this length group hake occupied the second rank in food items and first rank in all other length groups, with the exception of 41-45 cm (third rank).

Opportunistic Feeding

A second mechanism for compensation is opportunistic feeding. Hake make vertical migrations to feed in mid-water or surface layer at night. The Peruvian hake constantly changes its diet depending on the abundance of prey items. Based on feeding, we can divide Peruvian hake into two length groups: up to 30 cm (juveniles) and 31 cm and above (adults). Between 1976 and1986, it was observed that the main food items for juveniles were euphausiids. The adult hake fed on fish (98% in terms of weight) and crustaceans (2%). The main food item for adult hake was sardine followed by bereche, anchovy (*Engraulis ringens*) and hake itself (Castillo 1984; Fuentes et al. 1989). Hake predation on sardine was strong in years not affected by El Niño events. This feeding pattern changed in the 1990s. Whereas

crustaceans (euphausiids) are still the main food item for juveniles, adult hake have changed their diet to hake, Myctophidae and unidentified fish species (probably rare abyssal species), with very little consumption or total absence of sardine and bereche (Verónica Blaskovic', pers. comm.).

Aggregation Behavior

In contrast to other demersal fish populations, (e.g., cod) Peruvian adult hake do not show very strong aggregation behavior, i.e., there is no tendency for high-density aggregations. Therefore, an increase in vulnerability is not expected with a decline in stocks. Increases in catch per unit effort of commercial fleets could be explained by technology improvements. A brief analysis of density frequencies of all available cruise data shows an increase in low and medium density frequencies in the 1990s and a decrease of the high-density frequencies (Fig. 3). The observed trend in high-density frequencies demonstrates that Peruvian hake has a different aggregation behavior than northern cod (*Gadus morhua*) (Hutchings 1996). This aggregation pattern means an additional comparative advantage for hake, because part of the commercial fleet may not be able to exploit the stock.

Other Compensatory Mechanisms

A second group of compensatory mechanisms deals with life history parameters like life span, growth and size at maturity. In most models of population dynamics these are assumed to be static but have been proven to be non-static for Peruvian hake in at least one case.

Maximization of Fecundity

The length at first maturity is changing with decreasing stock abundance in Peruvian hake. Fig. 4 shows this as a percentage of changes in gonadal maturation in individuals less than 35 cm. As a long-lived species, hake is capable of having up to 15 year classes coexisting (i.e., ages 1-15 years) if only lightly exploited. Considering that sexual maturity was normally reached between 3 and 4 years in a lightly exploited population, an individual might spawn more than five times before dying of natural causes (M assumed to be 0.3 yr^{-1}). Thus species that spawn over several breeding seasons will be buffered against environmental fluctuations.

Furthermore, in each successive breeding year hake increase in body size and are expected to produce eggs of larger diameter like cod and haddock (Hislop 1988; Kjesbu 1989). It is expected that the quality of larvae improves with increases in parent body size. Like many other species, potential fecundity for European hake increases with fish length from about 100 000 eggs for a female 60 cm long to about 350 000 for a 100 cm specimen (Casey and Pereiro 1995). Actually, in the absence of older individuals, fishes of small body sizes that were reproductively inactive up to the 1980s, produce eggs and spawn in Peruvian hake stocks (Fig. 4). Thus, the number of spawners has increased as a mechanism to make up for the reduction in fecundity. Gould (1977) notes that a 10% decrease in age at first reproduction can often yield the same effect as a 100% increase in fecundity. It is not known if small hake produce only small eggs or whether they produce fewer large eggs.

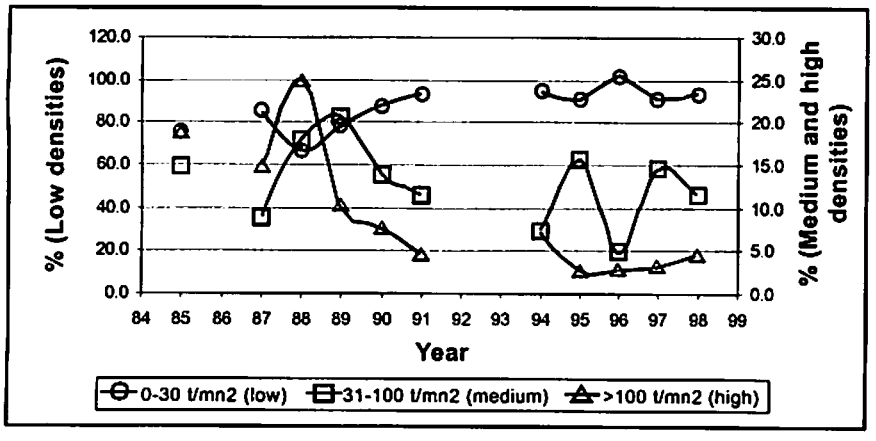

Fig. 3. Density frequencies in Peruvian hake surveys.

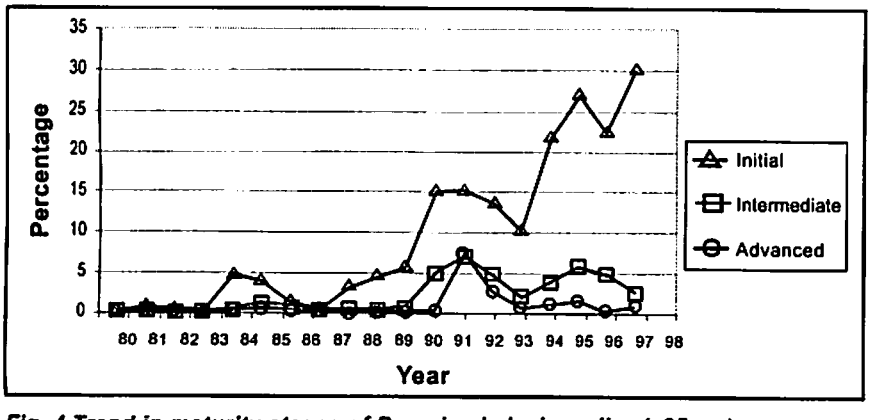

Fig. 4.Trend in maturity stages of Peruvian hake juveniles (<35 cm).

A hypothesis on what event leads to gonadal maturation and subsequent spawning in fish was presented by Pauly (1984). He argues that a constant ratio of Q_m/Q_u of about 1.4 exists (Q_u being the relative oxygen supply just sufficient for maintenance of metabolism and Q_m the oxygen supply near first maturity). Environmental changes provoked by physical or biological factors may act on fish by increasing Q_u and decreasing maximum length. With a constant Q_m/Q_u as a regulator, however, fish adapt to this by spawning at a smaller size.

Spatial and Temporal Refugia

Last but not least, like many other species Peruvian hake persist due to spatial and temporal refugia. The normal range of the fishing fleet is from 4° to 7°S. The bigger individuals further north are thus protected under a natural fishing ban and act as a spawning reserve, as do aggregations in deep-sea holes at >300 m depth that are not accessible to fishing gears.

Temporal refugia are also determined by the occurrence of ENSO events (wider distribution leading to decreasing concentration) and by cold years when hake follow the retreating Cromwell Current branches northward and northwestward as observed in the June 1996 (Guevara-Carrasco 1997) and January 1999 cruises (Fig. 5).

During a cruise executed while an extraordinary ENSO event was occurring in 1997, two different stocks of hake were found off the Peruvian coast (Guevara-Carrasco and Wosnitza-Mendo 1997). The northern (seaward) stock is normally not available to the trawl fleet and could constitute a spatial reserve for the southern stock. So far evaluation and management of stocks do not include the two stock hypothesis.

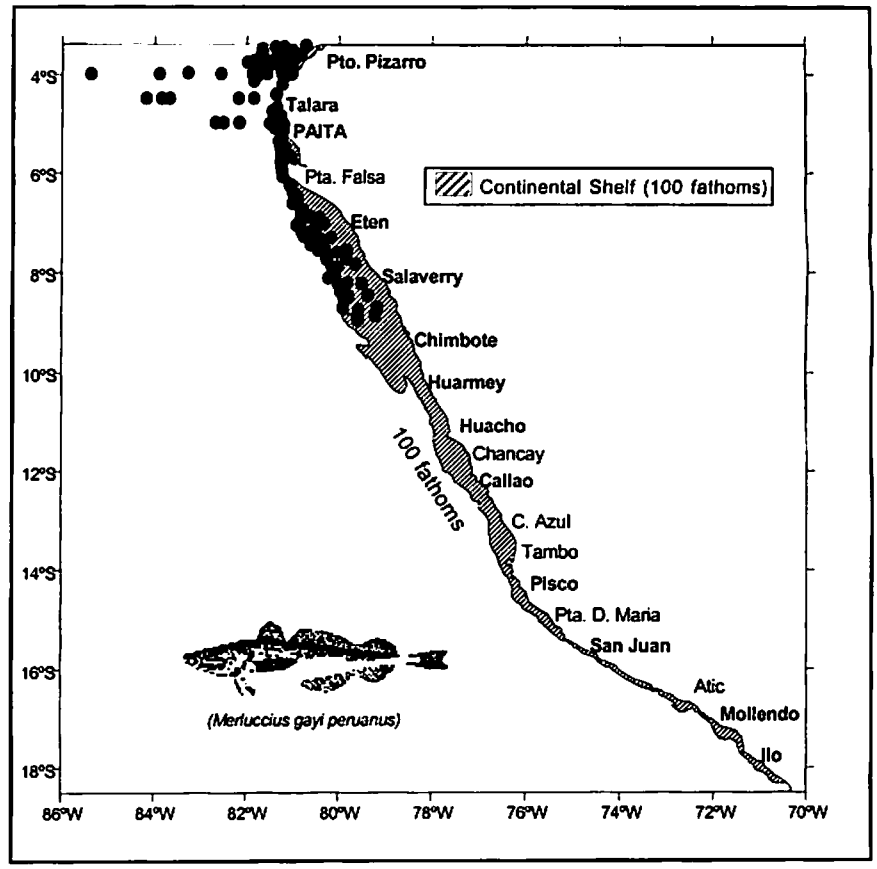

Fig. 5. Appraisal surveys of 1996.

Conclusions

The Peruvian hake population persists despite excessive fishing effort (acting since 1992 mainly on the younger part of the stock) due to various adaptive mechanisms. Adaptation is a holistic phenomenon involving many parameters and their interactions. Organisms adapt not only by altering their size and shape but also by adjusting the timing of their lives and the energy invested in different activities (Gould 1977).

Corresponding with the assumptions underlying r-K selection theory, changes in natural mortality must be considered. Jones and Johnston (1977) assumed that body size and age at maturity interact with natural mortality in such a way that the total reproductive output per individual is maximized. Roff (1984) hypothesizes that these interactions are the result of evolutionary adjustments due to the trade-off among reproduction, growth and survival, assuming a "cost" of reproduction. But both studies treat these aspects comparatively in different teleosts and do not discuss a shift in the same species, which is becoming more and more important in the last few decades. Heavy exploitation provokes environmental change not from resource limitation but from limitation by disturbance (Estes 1979). Trippel (1995) argues that shifts in maturity in many species which bear high levels of exploitation, are most likely to be a consequence of a mix of factors having both compensatory and genetic origins.

An increase in natural mortality in Peruvian hake can be expected considering several aspects discussed above:

- earlier gonadal maturation channels energy away from growth

and reduces survival probability;

- increased cannibalism might raise natural mortality rate to more than 0.3 as estimated in the 1980s; and
- the change in diet from sardine as prime component to Myctophidae and rare abyssal species might have increased natural mortality at least in the phase of adaptation.

Considering the stress that Peruvian hake is suffering from fishing pressure and changes in species interaction, the question is how long will this population continue to adapt and maintain a level of reproductive capacity to ensure its continuity. In addressing the problem of the hake fishery, biological reference points must be established to protect against stock collapse taking into account the conceptional relationships among community ecology, life history parameters and fishing pressure.

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