

Mechanisms for Density-Dependent Growth in Peruvian Anchoveta: Alternatives to Impact on the Regional-Scale Food Supply

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BAKUN, A. 1989. Mechanisms for density-dependent growth in Peruvian anchoveta: alternatives to impact on the regional-scale food supply, p. 235-243. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.) *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Two alternate classes of mechanisms that could account for evidence of density-dependent growth are introduced: (i) effects of potential linkages of school size with population size, and (ii) effects of size-dependent predation. These may lead to different interpretations with respect to resilience to exploitation, carrying capacity of the habitat, etc., from those implied by the more commonly cited class of mechanisms which involve impact of the population on its food supply.

Resumen

Dos mecanismos alternos que evidenciarían la denso-dependencia del crecimiento son introducidos: (i) efectos de relaciones potenciales del tamaño del cardumen con el tamaño de la población y (ii) efectos de la dependencia del tamaño con la predación. Estos pueden conducir a diferentes interpretaciones con respecto a la repercusión para la explotación, capacidad de carga del hábitat, etc., de aquellas implicadas por las clases de mecanismos más comúnmente citadas que abarcan el impacto de la población sobre su suministro de alimento.

Introduction

An apparent dependence of growth on population density is a common finding in studies of the dynamics of natural fish populations (e.g., Beverton and Holt 1957; Ware 1980). The mechanism commonly proposed involves increased competition for available food at high population density.

In the case of small coastal pelagic fish such as anchovies and sardines inhabiting coastal upwelling systems, the extent to which this type of mechanism might really be acting is not clear. For example, Lasker (1970) estimated that at peak population size, the Pacific sardine would have consumed more than the entire secondary production in California's current ecosystems. Nevertheless, no growth increase was noted among adults as the population declined (Murphy 1973). In the similar eastern ocean boundary upwelling ecosystem off Northwest Africa, Mathisen et al. (1978) compared food consumption to food production. Results suggested that food does not directly control the size of adult or recruited fish populations. Mathisen et al. cited Gulland (1971), Murphy (1973) and Steele (1974) as having questioned food limitation as a

control for adult fish "since in those cases where fish have been reduced to a low level through fishing, the structure and size of the next lower trophic level has not changed drastically". In the case of the Peru Current upwelling system, Lasker (1989) estimates that the anchoveta population, at a pre-collapse biomass level of 20 million t, would consume about one-fourth of the primary production of the ecosystem (note that the value "40", rather than "4", in Lasker's published paper is apparently a typographical error). Since anchoveta obviously will consume some quantity of secondary production, the question as to whether it may at times be limited by its food supply is unanswered.

Indeed, Palomares et al. (1987) found a significant correlation between growth performance and population biomass of Peruvian anchoveta over the period 1954-1982. They discussed three different effects which might have increased growth rates as the population declined: (1) decreased competition for available food due to fewer competing individuals, (2) a relative increase in abundance of more nutritious zooplankton, due to lessened competition for food resources and lessened predation by anchoveta, *vis à vis* less nutritious phytoplankton, and (3) a corresponding increased proportion of more efficient particulate feeding on zooplankton relative to less efficient filter feeding on phytoplankton. All three effects fall under the class of mechanisms implying a substantial impact of feeding activity on the amount or composition of the regional-scale food supply. Since natural mortality is generally size-dependent, and therefore growth-dependent, such a directly-linked impact of the population on its own food supply would seem to constitute a powerful compensatory mechanism with respect to effects of fisheries exploitation.

The purpose of this chapter is to point out that plausible alternative mechanisms exist which do not necessarily imply a substantial impact on the large-scale food supply. Two classes of mechanisms will be addressed: (1) effects of school size, and (2) effects of size-dependent predation. These may lead to different interpretations of evidence of density-dependent growth with respect to resilience of the population to exploitation, potential carrying capacity of habitat, etc.

Effects of School Size

Consequences of Fish School Geometry

As fish schools vary in diameter, they may also vary correspondingly in vertical thickness, i.e., large schools may be thicker in vertical dimension than small schools. To the extent that school thickness may vary in rough proportion to school diameter, the areal aspects of the school geometry, such as the surface area encompassing the volume occupied by the school or the cross-sectional area swept by school movement, will vary as the second power of δ (where δ = school diameter or other appropriate characteristic length scale). However, the volume of the school, and therefore, the number of individual fish contained, will vary as the third power of δ . Thus,

$$\frac{\text{school surface area}}{\text{school volume}} \propto \frac{\text{cross-sectional area swept}}{\text{no. of individuals in school}} \propto \frac{1}{\delta} \quad \dots 1)$$

The consequence of expression (1) is that as δ (i.e., school size) increases, the average supply per individual within the school of food and other substances (e.g., replenished dissolved oxygen where concentration may have been depleted by respiration) that must enter the school interior through the cross-sectional area swept by a moving school (or diffused through the outer surface area of a stationary school) decreases in proportion to δ^{-1} . Thus, a fish in a larger school (of size $\sim \delta_1$) must, in comparison to a fish in a smaller school (of size $\sim \delta_2$), either accept an average food ration which is smaller by the factor δ_2/δ_1 (and to the extent that a school may be capable of depleting the oxygen within the water volume occupied, the additional detriment of a lowered uptake rate of oxygen) or carry the metabolic costs of swimming faster by a factor of

δ_1/δ_2 . Kils (1979) discussed this effect as a factor limiting the school size of the Antarctic krill *Euphausia superba*.

Of course, it is possible that large schools are strictly limited in the vertical dimension by external constraints (water column structure, total water depth in shallow areas, vertical distribution of food organisms, etc.). In the case of a flattened school shape of constant vertical dimension, the volume and the surface area of a school vary nearly in direct proportion. Even so, the ratio of cross sectional area swept to the volume of a moving school would continue to vary as δ^{-1} so long as both horizontal dimensions tend to increase or decrease together (i.e., excluding the case where the length of the school axis parallel to its motion remains constant while school width, normal to the direction of motion, increases.) Actually, Mais (1974) finds seasonal, diurnal, and other (e.g., relation to topography) tendencies for school sizes and for school thicknesses to vary somewhat in phase, such that thicknesses of larger schools of northern anchovy off California tend to be greater than those of smaller schools. However, one finds little information in the literature on school thickness in relation to school diameter; this may indicate a lack of appreciation of the potential importance of school surface to volume ratios with respect to nutrition and metabolism of schooling fish.

Should Average School Size Increase with Population Size?

Pitcher (1986) cites potential advantages of schooling behavior in fish including hydrodynamic advantages, countering predation, discovery of food patches, and opportunities for group learning. In any case, it seems clear that for species with pronounced schooling behavior, individuals or small groups of fish must tend to increase their probability of survival and successful propagation of their genetic material by joining with other conspecific groups of similar body size that might be encountered. Thus, in the absence of processes tending to fragment the school, school size would tend to increase with time. The expected rate of increase depends on the rate of encounter with other individuals or schools; that is, all other factors being equal, it should be roughly proportional to population density, i.e.,

$$\begin{array}{l} \text{number of individuals joining} \\ \text{a given school per unit time} \end{array} \propto P^c \quad \dots 2)$$

where P is the size of the population, and the exponent c ($0 < c \leq 1$) represents MacCall's (1980) suggestion for incorporation of variable habitat size in representing a density-dependent mechanism (i.e., $c = 0$ implies that habitat size varies in proportion to population size and thus, that population density does not vary with population size; $c = 1$ implies that there is no habitat size variation and thus, that population density varies directly with population size; $0 < c < 1$ implies the less-than-proportional increase of habitat size with population size which, for coastal pelagic fish populations, appears to fit observations).

Obviously, processes tending to fragment schools become substantial at some point or the entire population would tend to aggregate into a few very large schools, whereas large numbers of disjoint schools is the observed situation. This implies that, while the tendency for aggregation must dominate when the school size is small, processes of fragmentation must become increasingly important as school size increases, i.e.,

$$\begin{array}{l} \text{number of individuals leaving} \\ \text{a given school per unit time} \end{array} = F(N) \quad \dots 3)$$

where $F(N)$ is some increasing function of N (N = number of individuals in a school), at least over an observed range of school sizes. Combining expressions (2) and (3) yields

$$\frac{dN}{dt} = kP^c - F(N) \quad \dots 4)$$

where k is the constant of proportionality implied by expression (2). Using a formulation equivalent to equation (4), Anderson (1981) added the assumptions that the number leaving was linearly proportional to N (i.e., $F(N) = K N$, where K is a constant) and that the number joining (kP^c) was constant with time. He added stochastic terms to the entrance and exit rates and to the relationship of N to δ . He thereby constructed a model that reproduced the frequency distribution of pelagic fish school diameters off Southern California reported by Smith (1970).

The question of the form of $F(N)$ is an important one. There must be some ultimate limiting point at which the school size becomes too large for its members to meet their metabolic requirements. Upon growing to that point, it would seem that the school must become unstable and break apart. However, Smith (1981) reports a substantial range of school sizes of coastal pelagic fish rather than the tight modal distribution that would suggest that school size is controlled only by the ultimate metabolic limit. Apparently, other processes of fragmentation act over a range of sizes well below that point.

The hypothesis that individuals altruistically leave the school when they perceive that it is becoming too large for peak efficiency appears to be untenable. A principle of behavioral ecology states that animals do not sacrifice their own fitness for the good of their group (e.g., Grafen 1984). Various models (Sibly 1983; Pulliam and Caraco 1984; Clark and Mangel 1984) indicate that the optimum group size is unstable and that group sizes in natural systems are considerably larger than optimal size. This is because individuals do better in a group (even an oversized group), than on their own. Pitcher (1986) draws the analogy to an overcapitalized fishery in which individuals will not withdraw in order to increase the profit of those remaining in the fishery as long as they themselves have not reached the point of zero profit. The effect of natural selection is to ensure that individual fish within a school maximize the probability of successfully propagating their own genetic material relative to that of other individuals in the school. Natural selection would thus act to obliterate this type of altruistic behavior.

Having rejected the hypothesis that altruistic behavior by individuals provides the mechanism for removing fish from a school, it is difficult to envision behavioral responses that would induce other individuals to exit the school while allowing the initiators to stay. The remaining possibilities include stochastic effects such as amplified random motions within a school that might lead to polarized movements in different directions by different segments of a school such that fish in between must relinquish their attraction to one of the segments to stay with the other. The two segments could thereby lose contact, thus splitting the school into two smaller schools. A related effect might occur when two separate food patches are encountered at two sides of the moving school front. Feeding behavior would attract school members to one or the other of the food patches, leading to a similar loss of contact between school segments (Paul E. Smith, pers. comm.). Also, it is possible that predator attack could fragment a school, although Pitcher (1986) emphasizes that the observed tendency under attack is for increased school cohesiveness.

In these cases, the average number of fish leaving a school per unit time should, on average, be proportional to the total number in the school at the time a fragmentation occurs; i.e., $F(N) = K N$ (where K is a constant of proportionality), as assumed by Anderson (1981). With this substitution, the equilibrium solution to equation (4) is $kP^c = K N$, or

$$\text{equilibrium school size} \equiv \tilde{N} = \left(\frac{k}{K}\right) P^c \quad \dots 5)$$

Equation (5) predicts that average school size will increase with population size provided $c \neq 0$ (i.e., provided population density increases with population size.) In fact, even if k and K are not constants, the two premises: (i) that the rate of entry into a school increases with population size, and (ii) that the rate of leaving the school increases with school size, must lead to an equilibrium that shifts to larger school sizes as population size increases. Of course, the actual distribution of school sizes might reflect large, possibly highly nonsymmetrical, stochastic variability about such an equilibrium.

Mais (1974) found that the discrete daytime schools of northern anchovies off California tended to break up into scattering layers at night. This is in accord with the common pattern for clupeoids (Blaxter and Hunter 1982). This particular type of shift in school size and character does not necessarily imply altruism by individuals, but merely an alteration in attraction and

cohesion due to changes in visual acuity with the drastic day-night change in light. Different values of k and $F(N)$ in equation (4) resulting from the changed attractive and cohesive properties would lead to two different effective equilibrium school sizes depending on day or night conditions. Mais also found that the distribution of school sizes is somewhat dependent on season. Seasonal changes in behavior, food patch size spectra, etc. could result to variations in attraction to the school (i.e., in k) or in cohesiveness (i.e., in $F(N)$) leading to seasonal variation in \bar{N} . He also noted extremely large dense schools forming along steep bottom gradients of submarine canyons or escarpments. In this case, the topographic features could in themselves attract fish (i.e., act to effectively increase k on a very local scale) and provide points of orientation which could counteract the tendency for school fragmentation as a result of random motions of polarized school segments (thereby decreasing $F(N)$). The result would be a corresponding local increase in \bar{N} . In all of these cases, equation (4) could separately apply to each diurnal, seasonal, or local situation, with the net integrated result that average school size in the habitat would increase with population size.

Applicability to the Anchoveta

Jordan (1971) notes that anchoveta form large, dense schools during the daylight hours which break up at night into smaller feeding schools. This may be a simplification of a more complex situation similar to that described by Mais (1974) for the northern anchovy. However, it will be useful to discuss the problem on this basis. In that case, the considerations presented above could act on both scales: (i) in the formation of the large daytime schools from a background "population" of feeding schools, and (ii) in the determination of the size distribution of nighttime feeding schools from the background population of individuals. In both cases, the effective value of P in equation (4) could depend on the total population size and the considerations presented above could thereby hold.

In the case of food ration, the nighttime case seems to be the pertinent situation to consider. In the smaller "feeding schools", a proportional variation of vertical dimension with horizontal dimension is most likely. In a tank experiment wherein relatively large food particles induced the "particulate" (i.e., "biting") feeding response, Leong and O'Connell (1969) found that a 64-fish school of northern anchovies received substantially less ration per unit time at a given particle density than did schools of 16 fish and less. J.R. Hunter (pers. comm.) has observed that anchovies in smaller schools tend to be less polarized in their behavior and more apt to make excursions from the main school trajectory in order to take particles lying outside of the school's main path; in larger schools, the individuals seem more controlled by cohesive behavior and therefore, apt to get less ration per individual.

In the case of oxygen supply, the large densely-packed daytime resting schools may constitute a situation where effects on oxygen uptake affect the ability to metabolize, and thereby utilize for growth, food taken during the feeding period (Pauly 1981). This writer is aware of no measurements of oxygen depletion taken at sea within a school of clupeoids. However, McFarland and Moss (1967) measured oxygen depletion within schools of striped mullet (*Mugil cephalus*). They found a reduction of dissolved oxygen within all schools measured. The magnitude of the reduction correlated with school size, ranging up to 29% (in a school of size $\delta = 150$ m). Actual values of the reduction were in the range of 0.12-0.40 mg L⁻¹ for "small" ($\delta = 4-9$ m) schools, 0.50-0.80 mg L⁻¹ for "medium" ($\delta = 18-30$ m) schools, and 0.70-2.10 mg L⁻¹ for "large" ($\delta = 75-300$ m) schools. Typical separation between fish within daytime anchoveta schools is of the order of one fish length (Jordan 1971) and so comparable reductions in dissolved oxygen concentration seem possible for large anchoveta schools. Brett (1979), in experiments with different fish species, found that a drop of dissolved oxygen of one mg L⁻¹ causes a 30% reduction in growth rate.

Effect of Size-Dependent Predation

Small coastal pelagic fish such as anchovies attract a varied community of natural predators including sea birds, marine mammals and predatory fish. These predators tend to live longer than

their smaller prey, and thus their population responses would tend to lag variations in their food supply. In many systems the predators have access to alternative prey. Switching of predation pressure to these alternate food resources is one likely response to population decline of a major prey species. But, because of the enormous size of the Peruvian anchoveta population prior to the 1971/72 collapse, and its corresponding dominance within the current Peru ecosystem, the opportunities for switching to alternative prey during the decline of the anchoveta might have been more limited than in more diversely populated ecosystems. Thus, predators without an option of migration to other feeding grounds, e.g., sea birds, marine mammals, etc., with strong local affinities, may have to attempt to derive continued sustenance by extracting an increased share of a declining food base.

On the other hand, predator populations that habitually migrate to exploit spatially separate food bases may not have to experience population declines due to decline in one of its major food bases. For example, Muck and Sanchez (1987) consider mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) the most important predators of anchoveta throughout the entire era of high anchoveta biomass and the more recent era of lowered biomass. These fish exploit both the nearshore habitat of the anchoveta and the habitat further offshore. They are opportunistic feeders, shifting to zooplankton and euphasids where anchoveta are less available. In fact, Muck and Sanchez (1987) assume a constant biomass of mackerel and horse mackerel over the entire period of high anchoveta biomass and recent decline, and thereby infer a relative increase in specific predation rate in the recent period.

These considerations suggest a substantial increase in natural predation pressure on the anchoveta, per unit anchoveta biomass, since the decline. If, as suggested in the previous section, school size has also declined, this could further increase predation mortality (if one accepts the argument of Clark (1974)).

Predation mortality is thought to be size-dependent in both larval (Hunter 1971; Folkvord and Hunter 1986; Miller et al. 1988) and juvenile (Parker 1971; Healy 1982; Hargreaves and LeBrasseur 1986) fish. Thus, animals which grow quickly through the various vulnerable stages increase their chances of successful recruitment. Any larva or juvenile which by chance gets access to a better ration or other favorable growth condition thereby acquires an incrementally increased probability of avoiding predation. This effect cascades as the fish grow through the multitudinous series of size increments between hatching and recruitment, with the net result that slower-growing individuals make up a reduced portion of the survivorship as age increases. The mode of the distribution of size at age is shifted toward larger sizes (Fig. 1). Thus, the apparent growth rate computed from samples of survivors would be larger than the true growth rate, merely because of the biased mortality.

For example, Parker (1971) experimented on replicate populations of juvenile salmon in eight separate aquaria each having an identical, continually replenished food density. Thus, the true growth rates should have been identical. In half of the aquaria, three larger salmon were introduced as predators; the other half were kept predation-free as controls. After allowing time for the populations affected by predation to be substantially reduced, all the populations were measured. An increased growth rate of 0.3-0.5% per day was measured in the populations affected by predation, due entirely to the bias caused by size-dependent predation.

If, as suggested earlier, the relative predation pressure was indeed increased during the population decline of the anchoveta, this bias toward larger size at age and corresponding larger apparent growth rate would have been amplified. In such case, there is no need for alteration of actual growth rates to have occurred in order to produce the evidence of density-dependent growth in anchoveta reported by Palomares et al. (1987).

Discussion

Three classes of hypothetical mechanisms for density-dependent growth have been put forth for consideration:

1. Impact of the population variations on the ambient food supply,
2. Effects of linkages of school size with population size,
3. Effects of amplified size-dependent predation during population decline.

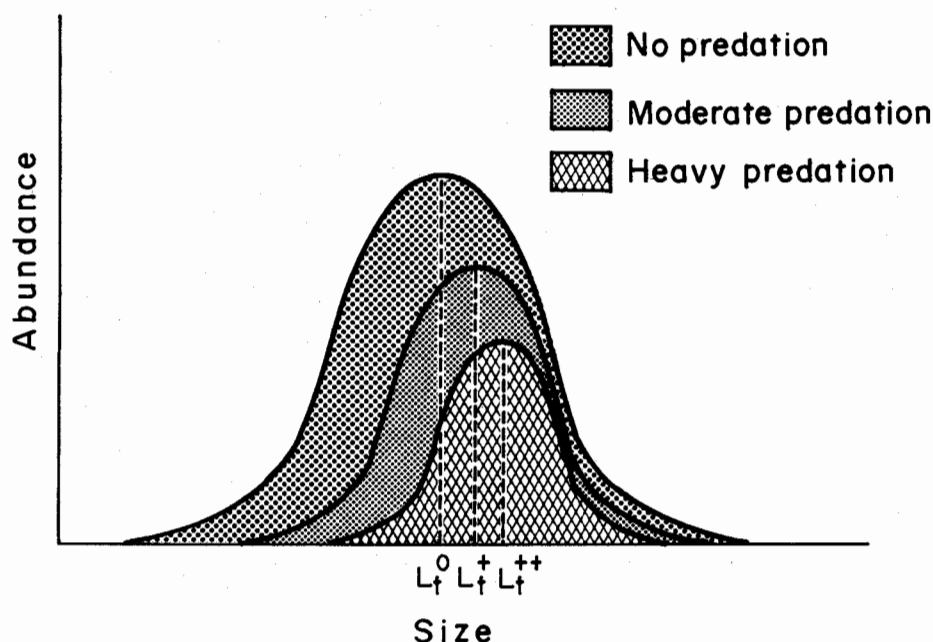


Fig. 1. Illustration of the apparent shift to larger size at age due to size-dependent predation. Where, if there had been no mortality due to predation the observed mean size at age "t" may have been L_t^0 , at a moderate level of predation it would be L_t^+ . If predation mortality is increased, the abundance at age is lowered further, the distribution is shifted toward larger sizes and the observed size at age would be L_t^{++} . The result is: $L_t^0 < L_t^+ < L_t^{++}$.

Fig. 1. Ilustración del cambio aparente a tamaños mayores en una edad debido a la predación dependiente tamaño. Donde, si no ha habido mortalidad debido a predación el tamaño promedio observado a una edad "t" puede haber sido L_t^0 , a un nivel moderado de predación este sería L_t^+ . Si la predación es incrementada, la abundancia a una edad es reducida además, la distribución es cambiada hacia mayores tamaños y el tamaño observado a esa edad sería L_t^{++} . El resultado es: $L_t^0 < L_t^+ < L_t^{++}$.

The first class is the one often considered. It has the comforting implication that, since the population would appear to be effectively eating up its food supply at high biomass, there must be substantial surplus production and associated compensatory resilience to exploitation. The second class of mechanisms also has compensatory implications, but does not imply, as does the first, that the population at high biomass may be nearing the limit of the carrying-capacity of its habitat. The third class of hypothetical mechanisms is not comforting at all, implying nothing but increased predation mortality during a population decline, i.e., a depensatory density-dependent process rather than a compensatory one.

In addressing the potential effect of school size, the relationship of vertical thickness to horizontal scale is a crucial aspect. To the extent that vertical and horizontal aspects may be functionally linked, important consequences of school size to nutrition, growth and metabolism are indicated. In fact, a general tendency toward vertically-flattened school shapes (Blaxter and Hunter 1982) may constitute an adaptation to avoid some of these consequences. Information on this functional linkage is surprisingly absent in the literature, although it would seem not difficult to acquire.

If there is a "moral" to this contribution, it illustrates the need for an "integrated ecosystem" view of marine resource population dynamics. We have seen the possibilities of three different interpretations of the same evidence, each with crucial, but highly differing, implications to stock management and preservation. To a fisheries oceanographer, the situation feels familiar. It is not very different from the dilemma faced in attempts to empirically sort out marine biological-environmental linkage mechanisms when one finds, in the typical case, that the available time series relating to various causal mechanisms are all highly intercorrelated and autocorrelated (e.g., Bakun 1987; Mendelssohn and Mendo 1987). The result is that available information is simply too limited to empirically differentiate among the possibilities.

How can we expect to make progress in sorting out the factors controlling marine resource population variability? Clearly, we need innovative approaches. And we need to recognize,

integrate and utilize information on all the various scales, both spatial and temporal, that can be accessed. For example, this contribution indicates that in addressing issues of population ecology, it is important to consider processes occurring on the scale of the school (for that matter on perhaps two school scales, both of the nighttime "feeding" school and of the daytime "resting" school), as well as on the population habitat scale. To be blunt, fisheries science needs to expand beyond the "giant guppy tank" concept of an ecosystem, and relinquish the conventional "one-spatial/temporal aggregate-data-point-per-year" approach to variability, so as to be capable of utilizing all the information in the rich patterns of variation within years, and both within and among regions (Bakun, in press). The cooperative assembly and integrative analysis of various types of data reported in this volume and in the earlier companion volume (Pauly and Tsukayama 1987) can perhaps serve as a model in this direction, both in the attempt to address variability of higher than annual frequency, despite difficulties caused by interferences related to seasonal tuning of various processes, and in its making readily available the basic data for use by anyone with an innovative idea. If the concept were to be emulated in other regional systems, the comparative method of science (Mayr 1982) might constitute a potent tool for increasing the power of empirical analysis (Bakun 1985).

Acknowledgments

Discussions with John R. Hunter, Paul E. Smith, Gary D. Sharp and Richard H. Parrish have been extremely helpful in organizing my ideas for this contribution. However, any errors of naiveté or oversimplification are certainly my own.

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INSTITUTO DEL MAR DEL PERÚ (IMARPE)
CALLAO, PERÚ

DEUTSCHE GESELLSCHAFT FÜR TECHNISCHE ZUSAMMENARBEIT (GTZ), GmbH
ESCHBORN, FEDERAL REPUBLIC OF GERMANY

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

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Proceedings of the Workshop on Models for
Yield Prediction in the Peruvian Ecosystem,
24-28 August 1987, Callao, Perú

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FEB 08 1991

EDITED BY

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P. MUCK
J. MENDO
I. TSUKAYAMA

1989

Published by Instituto del Mar del Perú (IMARPE), P.O. Box 22, Callao, Perú;
Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Postfach
5180, D-6236 Eschborn 1 bei Frankfurt/Main, Federal Republic of Germany;
and International Center for Living Aquatic Resources Management (ICLARM),
MCP.O. Box 1501, Makati, Metro Manila, Philippines

Printed in Manila, Philippines

Pauly, D., P. Muck, J. Mendo and I. Tsukayama, Editors. 1989. The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM Conference Proceedings 18, 438 p. Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

ISSN 0115-4435
ISBN 971-1022-47-8

Cover: False color satellite images of the Peruvian upwelling system taken during a 4-day period (5-8 May 1985) with a well developed area of cold waters along the Peruvian coast (front cover) and during a 3-day period (2-4 March 1986) when warm oceanic waters invaded the nearshore habitat of anchoveta (back cover). (Images: courtesy of the US National Oceanic and Atmospheric Administration).

PROCOPA Contribution No. 92
ICLARM Contribution No. 409

8775