

Physical, biological and fisheries oceanography of a large ecosystem (west coast of Vancouver Island) and implications for management

Ocean climate Species interactions Pacific hake Pacific herring Trophodynamics

Climat océanique Interactions entre les espèces Colin du Pacifique Hareng du Pacifique Dynamique de la nutrition

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# ABSTRACT

The west coast of Vancouver Island is one of the most productive fishing grounds off western North America. In 1985, a multi-disciplinary study was initiated to provide long-term physical and biological data from this large marine ecosystem that could be used in the development of management strategies for commercial fish stocks. In this paper we review the physical, biological and fisheries oceanography of this system. We use this information to examine the linkages between these components, particularly changes in abundance of major fish species in relation to physical and biological oceanography. In addition, we present an overview of a model developed to synthesize our current knowledge about this ecosystem and the relative importance of climate conditions and predator-prey relationships in determining interannual and longer-term variation in productivity.

RÉSUMÉ

Physique et biologie des pêches dans un grand écosystème marin (ouest de l'île Vancouver) et conséquences pour sa gestion.

La côte ouest de l'île de Vancouver est l'une des zones de pêches les plus productives à l'ouest de l'Amérique du nord. Un programme pluridisciplinaire lui est consacré depuis 1988 pour acquérir des séries de données à long terme en physique et en biologie, en vue de développer des stratégies de gestion des réserves commerciales de poissons. Le présent travail analyse les relations entre ces données, et en particulier les variations d'abondance des principales espèces de poissons. Un modèle fait le point des connaissances sur cet écosystème, sur le rôle des conditions climatiques et sur les relations entre proies et prédateurs dans la variation interannuelle et à long terme de la productivté.

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# INTRODUCTION

Most fisheries assessments are still based on the premise that there is a single, stable stock optimum that can be sustained. There is an implicit assumption that the environment is in equilibrium or has only minor or short term variation. For the most part these single species assessments have not provided the scientific basis to ensure rational development and management of fisheries.

It is becoming increasingly recognized that climate and ecosystem variation is controlling productivity in our oceans, and recruitment and distribution of our major fish species, on both an interannual and decadal time scale. Understanding this variation and its impacts on our resources is the most important question facing fishery scientists in the next century.

In the North Pacific Ocean the dynamics of ocean circulation, and in turn ocean productivity is forced on both interannual and decadal time scales by the strength of the Aleutian Low Pressure system, which dominates the north Pacific in winter. Deep nutrients in the north Pacific waters are advected coastward and upwelled on the continental margin west of Vancouver Island (McFarlane and Beamish, 1992; Beamish and Bouillon, 1993). This interannual and decadal climatic variability influences the physical ocean environment in coastal areas (Fig. 1) and subsequently the productivity of coastal ecosystems. Decadal scale shifts in fish abundance (Hollowed, 1990; Ware, 1991; Beamish and Bouillon, 1993) and zooplankton (Brodeur and Ware, 1992) have been related to these shifts in ocean productivity.

The La Perouse project is a multi-disciplinary, multispecies investigation conducted by the Pacific Biological Station and the Institute of Ocean Sciences. The primary focus of the program has been directed toward describing and understanding the causes of annual and interannual variability of the fish and zooplankton stocks over La Perouse Bank on the southwest portion of the shelf (Fig. 2). The most important goal of the La Perouse project is to improve the ability of the Department of Fisheries and Oceans to make accurate forecasts of multispecies fish production and potential yields a few years in advance. This would provide considerable benefits to the commercial fishing industry by minimizing potential fishery conflicts, and by optimizing the catch quotas to the general level of productivity in the system.

The principal objectives are to determine the key physical and biological factors that effect commercial fish population distributions, abundances and natural mortality rates; to determine the dominant predator-prey relationships in this productive upwelling ecosystem and to use measurements of spatial and temporal distributions of



Figure 1

Average annual sea-surface temperature at Amphitrite point (1934-1993). Horizontal line represents the long-term mean (10.4/).

predator and prey stocks to model the principal interactions in the system; to use the emerging scientific results from the program to develop and verify biophysical models that can be used as operational tools in the long-term planning and management of the multispecies fisheries off the west coast of Vancouver Island.

## STUDY AREA

The La Perouse Bank region is located at the northern terminus of the North American West Coast coastal upwelling domain (Ware and McFarlane, 1989). This production system is characterized by a relatively narrow continental shelf, intense wind-induced upwelling in summer, and high phytoplankton and euphausiid biomass. This high production is supported by three sources of



Figure 2

La Perouse Bank survey region (southwest coast of vancouver Island).

nutrient supply: 1) wind-induced upwelling along the outer shelf and subsequent cross-shelf mixing into the nearshore surface layer; 2) transport of nutrient-rich water seaward from Juan de Fuca Strait; and 3) wind-induced upwelling at the northern tip of Vancouver Island and subsequent alongshore transport of nutrients and plankton by the equatorward flowing shelf-break current. Zooplankton biomass tends to be highest in the Juan de Fuca Eddy and along the shelf-break and slope, and is dominated by calanoid and cyclopoid copepods and euphausiids (Mackas, 1992). This rich plankton community supports resident pelagic and demersal fish stocks, as well as a large, migratory stock of Pacific hake that travels from California to La Perouse Bank to feed in summer (June-October).

# Physical oceanography

The physical oceanographic component of the project provides current and water property data along the west coast of Vancouver Island and in the western portion of Juan de Fuca Strait in support of fisheries and interannual climate investigations. The physical data also describe the circulation dynamics over the shelf and provide a data base for El Niño related oceanic variability.

# **Regional circulation**

The west coast of Vancouver Island borders the bifurcation zone of the *Subarctic Current*, an extensive zonallyflowing, cross-Pacific surface current which originates off the coast of northern Asia (Dodimead *et al.*, 1963; Tabata, 1975). To the west of Vancouver Island, it splits into the poleward flowing *Alaska Current* and the equatorward flowing *California Current* (Fig. 3). There is also a nearshore undercurrent (the California undercurrent) which flows poleward throughout the year at depths greater than 200 m.

# Seasonal variability

Southeasterly winds dominate the region during winter, causing onshore transport, downwelling and poleward transport of surface waters (Dewees and Strange, 1984). During summer, upwelling is the prominent feature in the shelf-break region. It is caused by an intensification of the North Pacific high pressure system, and a corresponding shift to northwesterly winds. The prevailing upper layer circulation over the continental margin changes markedly during spring and fall in approximate concert with the annual reversal of the prevailing winds. The spring and fall transitions in the wind - and the ocean - are not gradual but take place quite abruptly over periods of a week or so. The Spring Transition generally occurs between late February and early May along with a major reversal of the prevailing winds along the coast. Associated with the wind reversal is a reversal in the direction of the current over the shelf-break, a lowering of mean coastal sea level, a re-stratification of the shelf/slope waters through increased



Figure 3

The prevailing currents off the west coast of Canada. The Subarctic Current splits into the poleward flowing Alaska Current and the equatorward flowing California Current (from Thomson, 1981).

warming and dilution of the near-surface shelf waters, and the onset of upwelling conditions over the outer-shelf.

# Interannual variability

Year to year variations in the shelf circulation arise through interannual changes in the prevailing winds, coastal runoff and outer shelf/slope circulation. Long-term fluctuations in runoff include changes in total volume as well as spatial variations in the runoff distribution along the coast. Thomson and Ware (1996) use an index of oceanic variability based on time series of currents to examine interannual variations in the onset times and duration of the oceanic seasons, and to quantify the intensities of winter downwelling and summer upwelling. For example, the winter downwelling/summer upwelling intensities prior to the 1991/92 El Niño event in the North Pacific were abnormally small while upwelling during the summer following that event was abnormally high. The index also suggests that the spring and fall transitions have longer duration than suggested by other indices.

Interannual differences in the timing and abruptness of the Spring Transition have an important impact on fish and invertebrate stocks in the region. Recent studies have linked the distribution and abundance of fish larvae (McFarlane *et al.*, 1995), adults (Ware and McFarlane, 1995), and invertebrate larvae (Jamieson *et al.*, 1989) to the timing and intensity of the Spring Transition and subsequent strength of the Vancouver Island Coastal current.

## **BIOLOGICAL OCEANOGRAPHY**

Macrozooplankton occupy a key intermediate position in the La Perouse Bank pelagic food web. They are the main consumers of large phytoplankton cells and microzooplankton which graze smaller phytoplankton. They are also the principal food for most pelagic fish, seabirds and marine mammals. Zooplankton community composition, biomass, and spatial distribution are therefore likely to play a significant role in the coupling between ocean "climate" and regional ecosystem response. We now know that very significant shifts in the total yield and structure of marine ecosystems can occur over interannual to decadal time scales. To examine the extent and cause of these changes, we have included both sustained time series "monitoring" and shorter-term "process study" research components in the program.

## Time series

Seasonal cycles of plankton and nutrients have been analyzed by Mackas (1992) and Mackas and Galbraith (1992). Figure 4 (from Mackas and Galbraith, 1992) summarizes the seasonal cycle of phytoplankton biomass from the three regions of the La Perouse area. Figure 5 (from Mackas, 1995) shows annual cycles of major zooplankton groups within one of the three La Perouse regions. Dissolved nutrients and resulting phytoplankton production and biomass are on average strikingly high throughout a prolonged upwelling season lasting roughly from April through October. A variety of physical processes contribute to this input and are discussed above. In general, the highest summer concentrations (5-9 FM NO<sub>3</sub>, 5.5-8.5 mg m<sup>-3</sup> Chl *a*) occur over the inner part of the continental shelf. Seaward of the shelf-break, average concentrations are lower but still substantial for marine waters (1-2.5 FM NO<sub>3</sub>, 0.8-3 mg m<sup>-3</sup> Chl *a*). There is much short-term variability about these averages caused by a sequence of several dense blooms during the upwelling season.

The zooplankton community off British Columbia integrates and smooths the rapid week-to-week cycling of phytoplankton biomass but still displays annual cycles in biomass and species composition (Fig. 5). Although the full local zooplankton community is species rich (100s of species), most of the total biomass and energy flow can be described with relatively few taxa (about twenty species within six phyla). Dominant taxa include euphausiids, herbivorous copepods, chaetognaths and gelatinous zooplankton. Amplitude and timing of the average seasonal cycle differ between shelf and offshore locations. Minimum biomass is in winter (about 1-2 g  $m^{-2}$ dry weight) in all regions. The maximum is in late spring on the continental shelf (7-8 g m<sup>-2</sup>), and in mid- to late summer seaward of the shelf-break (6-7 g  $m^{-2}$ ). The summer-autumn decline of herbivorous copepod biomass on the inner and middle parts of the shelf occurs during a period of sustained high food supply (3-8.5 mg m<sup>-3</sup> Chl *a*), and is evidence for rapid advective export of surface-layer zooplankton from the continental shelf during the summer upwelling season.



#### Figure 4

Thirteen-year average (1979-1991) seasonal cycle of zooplankton biomass and community composition in each of the three La Perouse zooplankton statistical regions. Most of the total zooplankton biomass is accounted for by about twenty species in the nine higher order taxonomic groups shown. There is a strong seasonal cycle in all three regions, but the regions differ in species mix and in the timing and duration of the biomass peak.



Time-series of annual anomalies for major zooplankton taxa in the southern shelf "gyre" region. Euphausiid anomalies show a strong trend of increasing biomass: negative anomalies 1985-1986 and positive anomalies 1989-1990. the "shelf" copepods Calanus marshallae and Pseudocalanus have large negative anomalies in 1986-1987. Neocalanus spp. have negative anomalies from 1987-1991. Chaetognath anomalies are mostly small for the dominant species Sagitta elegans but are frequently significant for the "oceanic" species Eukrohnia hamata and S. scrippsae.

Some of the observed year-to-year zooplankton changes are shown in Figure 5. Note that anomalies in biomass-withinspecies are expressed on a logarithmic scale. An anomaly of +0.3 represents an approximate doubling relative to the long-term geometric mean, an anomaly of -0.3 represents about half the long term average. To save space and show shared patterns, anomaly time series of taxonomically and ecologically similar species have been "stacked" in these

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graphs. What can be learned from these time series? Most of the dominant taxa show interannual deviations from the multiyear average seasonal cycle that are both statistically and ecologically significant. The anomalies last rather a long time (0.3-5 years depending on taxonomic group). Within-taxa, the anomalies tend to be larger along and seaward of the continental shelf break than on the continental shelf. Significant zooplankton anomalies occur throughout the time series; they are not confined to El Niño years. Both time scale and phasing of anomalies suggest coupling to longer term variations in North Pacific atmosphere-ocean conditions.

## **Process studies**

A major outcome of the process studies has been the repeated demonstration of strong associations between bathymetric, flowfield, and plankton distribution patterns. Adult euphausiids and their predators (several of the dominant finfish) aggregate strongly along bathymetric "edges" and accompanying zones of current shear and convergence (Simard and Mackas, 1989).

Along shore and cross-shore transport has a major effect on plankton population dynamics, both as a source for nutrients, and an export mechanism for plankton biomass (Mackas, 1992). Satellite images and the trajectories of drogued buoys both show rapid alongshore flow at the continental shelf break, and occasional splitting of this flow to produce large seaward jets of continental shelf water (Emery *et al.*, 1986; Denman *et al.*, 1989).

## FISHERY OCEANOGRAPHY

Historically, fisheries off the west coast of Vancouver Island can be divided into pelagic (sardine, *Sardinops sagax*; Pacific herring, *Clupea harengus*; Pacific hake, *Merluccius productus*; and salmon, *Oncorhynchus spp.*), and demersal or groundfish fisheries. Catches averaged 30,000 t annually from 1920 to the mid-1960s and increased since to over 100,000 t since the late 1980s (Fig. 6).

The catch during the first fifty years was dominated by clupeoids. The Pacific sardine (or pilchard) fishery developed in the early 1920s and was the most important fishery in the region until its collapse in 1946 (Fig. 6). Since the demise of this stock, Pacific herring has become the most economically important pelagic species in the La Perouse region. Catches have fluctuated between <1000-38,000 t annually, and averaged 15,000 t over the last seventy years (Fig. 6). Since 1978 there has been a trend towards decreased catches (about 6,600 t annually), primarily due to poor recruitment (Schweigert and Fort 1994), caused by an intensification of the predation rate and possibly poorer feeding conditions (Ware and McFarlane, 1995).

The most dramatic change in the pelagic fishery occurred when a large stock of Pacific hake was discovered by the Russian trawl fleet offshore in the early 1960s. Since 1968, the largest catches have usually been hake (Fig. 6), averaging 42,000 t annually. After the Canadian extended



Figure 6 (A-C).

fishing zone was created in 1977, hake catches increased steadily to 100,000 t in 1989.

On average, during the 1980s, the La Perouse region supported about 390,000 t of fish biomass in the summer (Table 1). Pacific hake dominate the system, accounting for 61% of the biomass during summer. Hake is a migratory species which enter Canadian waters in late spring (May/early June) (Beamish and McFarlane, 1985) and feed in the deep basins of the continental shelf and along the shelf-break before returning south around the time of the fall transition. Hake show marked interannual variation in biomass (Saunders and McFarlane, 1994) related to oceanographic conditions (Ware and McFarlane, 1995). Herring are a year-round resident of the La Perouse Bank region. They typically occur near the margins of the banks in depths of less than 100 m. These herring are from



Figure 6 (D-E) (continued).

Total landings of pelagic and demersal fish from the La Perouse Bank area 1920-1993. Total pelagic landings include sardine, herring, hake, chinook and coho salmon, and pollock (modified from Ware and McFarlane, 1995).

two stocks; the West Coast Vancouver Island stock and the Strait of Georgia stock.

About 67% of the herring on the west coast of Vancouver Island (25,000 t), and 50% of those in the Strait of Georgia (29,500 t) spend the summer feeding around La Perouse Bank. Thus in the 1980s, about 54,500 t of herring (age 2 + and greater) summered on La Perouse Bank (Tab. 1). During the 1980s, the west coast of Vancouver Island stock

#### Table 1

Average summer biomass of dominant pelagic and demersal fish species in the La Perouse Bank area during the 1980s. From Ware and McFarlane (1995).

Species	Biomass (10 tonnes)
Pacific Hake	236
Pacific herring	55
Dogfish	38
Coho salmon	15
Pacific cod	10
Sablefish	8
Chinook salmon	11
Lingcod	8
Rockfish spp.	6
Halibut	1
Total	388



Figure 7

August distribution (research trawl CPUE kg.  $m^{-3}$ ) of Pacific hake in 1983 (warm summer) and 1985, 1987, and 1989 (average summers) (Ware and McFarlane, 1995).





Relationship between average summer sea-surface temperature and swept-volume hake biomass estimates for fifteen survey years between 1968-93 (modified from Ware and McFarlane, 1995).





Weighted amount of herring in hake diet in August as a percentage of the body weight, with respect to sea surface temperature during the 1983, and 1985-1993 surveys. Sample values were weighted by the relative abundance (catch rate) of hake in the area of each sample (modified from Ware and McFarlane, 1995).

averaged 37,000 t, which is below the historical average stock size of 45,600 t. The reasons for this are discussed below.

# Key predator-prey interactions

Tanasichuk *et al.* (1991) examined the summer diet of the dominant fish species for eight years. Euphausiids and herring were the main prey. On average, these two food items make up 92% of the diet of hake (by weight), 70% of the diet of dogfish, and 89% of the diet of chinook salmon. Euphausiids were the dominant food of most of the predator species sampled, except for chinook salmon, where herring predominated.

Ware and McFarlane (1995) examined the relationship between hake distribution and abundance, and oceanographic conditions as reflected by sea surface temperature (Figs. 7, 8). They found that both distribution and abundance were strongly modulated by changes in water temperature, and that predation on euphausiids and herring were significantly related to changes in hake distribution and abundance. Their data indicated that the fraction of herring in the hake diet is a dome-shaped function of the local temperature (Fig. 9). Since euphausiid productivity and biomass tend to decrease with increasing summer temperatures (Robinson and Ware, 1994), Figure 9 implies that, up to a temperature of about 14.1°C, hake consumption of their secondary prey (herring) increases, as the availability of their primary prey (euphausiids) decreases. During years with the highest August temperatures, hake are distributed more northward, and along the outer shelf (Fig. 7) where herring are less available, consequently the fraction of herring in the August diet diminishes.

Robinson and Ware (1994) speculated that the natural mortality rate of all age-classes of herring is higher in warmer years. In general, coastal sea surface temperatures have been warmer than average since 1977 (Fig. 1). During this time there has been below average herring recruitment (Schweigert *et. al.* 1994), resulting in a decline in the west coast herring stock from 139,000 t in 1975 to about 32,000 t in 1993 (Schweigert and Fort, 1994). This relationship between herring stock size, and warm and cool temperature regimes has been a persistent feature of the historical herring recruitment time series (Ware, 1991).

Other studies in the La Perouse area have examined the relationship of year-class success of marine fish with physical and biological ocean conditions. McFarlane and Beamish (1992) reported that the production of strong yearclasses of sablefish, *Anoplopoma fimbria*, resulted when favourable climate/oceanographic conditions increased the amount of food available for larvae. When these conditions were favourable all other factors affecting year-class success were over-ridden. They also suggested that during most years, year-class variation in localized areas depended, in part, on physical oceanographic conditions; specifically, ocean circulation. McFarlane *et al.* (1995) surveyed the distribition and abundance of larval sablefish in the La Perouse area over a six-year period (1985-1989) and found that both were related to the timing and intensity of upwelling-favourable conditions during the spring transition.

## Trophodynamics model

A trophodynamics model has been developed (Robinson and Ware, 1994) to estimate average annual plankton and fish production in the La Perouse Bank area in relation to oceanic variability. Refer to Robinson *et al.* (1993) and Robinson and Ware (1994) for detailed discussions about model structure. The model is forced by intra-annual and interannual variability in upwelling, solar radiation, and sea surface water temperature, and by concentrations of major fish predators (Pacific hake, Pacific herring and Dogfish). The main abiotic and biotic interactions are summarized in Figure 10.

Results from the model simulations are the first published estimates of annual plankton and fish production for the region (Robinson et al. 1993). Using observed intra- annual and interannual variability in environmental conditions and fish concentrations, the model estimates that annual diatom production ranges from 250-500 (av: 345) g C m<sup>-2</sup> y<sup>-1</sup>, while copepod production ranges 5-50 (av: 17) g C m<sup>-2</sup> y<sup>-1</sup>, and euphausiid production from 7-20 (av: 14) g C m<sup>-2</sup> y<sup>-1</sup>. The Robinson-Ware model simulations also indicate that interannual and longerterm variability in coastal plankton production occurs, and that some years may favour copepod production versus euphausiid production and vice versa. The trends in annual plankton production are determined primarily by the dynamics in the initiation and intensity of spring and summer upwelling, which in turn are affected by atmospheric pressure systems (Robinson, 1994).

The simulations indicate that between 0.5% and 1.2% of the diatom production is transferred to hake and herring annually, and that fish production is linked to zooplankton



## Figure 10

Summary of the feeding interactions of the most abundant pelagic organisms in the Juan de Fuca Eddy region. Solid lines and arrows point to the predators of each prey, dashed lines and arrows point to the effects of non-trophodynamical processes. Note that water temperature affects diatom growth, all feeding interactions, and hake biomass. See Robinson and Ware (1994) for more details. dynamics. For instance hake production is mainly influenced by summer euphausiid production, while herring production is related to spring and autumn zooplankton production. Early results indicated that there was an imbalance between the production of euphausiids and the consumption of euphausiids by hake, herring, and dogfish during the upwelling season. Further simulations indicated that a relatively high adult euphausiid growth (>3.0% body weight d<sup>-1</sup>), in combination with oceanographic mechanisms that import and accumulate euphausiids in the Juan de Fuca Eddy region, were required to satisfy the high upper trophic-level demand for euphausiids.

An important process identified by model simulations is the dynamical interaction between euphausiids and hake (Robinson and Ware, 1994). Simulated hake biomass peaks at about 200 kt by early July before rapidly declining through the late summer to about 100 kt (Fig. 11). The seasonal pattern in euphausiid abundance was produced by adjusting the raw catch data in Figure 4 for day/night differences in euphausiid availability to the sampling gear (Robinson and Ware, 1994; App. 2). This pattern can be explained as follows: in early summer hake and other fishes consume a large biomass of accumulated euphausiids in the Eddy region, but by late summer the remaining euphausiid biomass is unable to support the trophic demands of the large pelagic fish biomass. Thus hake disperse from the Eddy region to surrounding oceanographic regions searching for new sources of prey (Ware and McFarlane, 1995; Robinson and Ware, 1994). It is during late summer and early fall that herring experience their greatest mortality from hake, as the latter search for new prey. The linking of hake migration to euphausiid concentrations in the model has allowed us explore the seasonal dynamics in euphausiid, herring, and hake feeding interactions. Inclusion of this dynamical function in the Robinson-Ware



#### Figure 11

Simulated annual biomass patterns of euphausiids and Pacific hake for the Eddy region during 1985-1989. See Robinson and Ware (1994) for more simulation results.

model was necessary to mimic the real-world behaviour of this pelagic ecosystem.

Simulation results indicate that two aspects of hake migration, biomass and time of arrival in southern B. C. waters, can strongly influence zooplankton and resident fish production dynamics, while only minimally influencing diatom production (Robinson and Ware, 1994). However when simulations incorporated the observed interannual variability in environmental forcing functions (upwelling, temperature, and light), it becomes apparent that physical oceanographic variability overrides the influence of biotic factors (predation) in determining system production. Interestingly, the relative interplay between resource limitation and predation changes seasonally and among years because oceanic variability influences the trophodynamical phasing between organisms in the pelagic food-web (*sensu* Parsons, 1988; Robinson, 1994).

## MANAGEMENT IMPLICATIONS

The La Perouse project has made substantial contributions to the assessment and management of fish stocks on the west coast of Vancouver Island. Specifically, the information linking the ocean environment to hake/herring interactions and herring recruitment is used directly in developing management strategies for herring. Perhaps the biggest contribution of this study is our ability to partition fishing effects from environmental effects for herring stocks. This was only possible because the project spanned a time frame (decade) which allowed us to examine interannual variation in herring production.

By identifying and forecasting regime shifts in the ocean climate and by understanding the relationship between ocean variability and production, distribution and recruitment of fish we will be able to provide a biological basis for changes in species dominance and productivity and for developing assessments and management strategies for commercially important species. For example, our understanding of the seasonal abundance, distribution and biological response of Pacific hake to local oceanic conditions has been used not only to assess the dynamics of hake in Canadian waters but directly in negotiations between Canada and the United States to arrive at equitable quotas for this transboundary stock.

In closing, understanding climate/oceanographic/fish linkages is a new area of multidisciplinary research. These studies require a long-term commitment by not only the researchers involved but also by governments who must ensure a rational and sustainable harvest of the resource. The La Perouse project has demonstrated that factors other than fishing can impact marine fish stocks and that identifying and understanding the dynamics of these factors is essential for management and for adapting management strategies in response to changes in ocean productivity.

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