Research Note

On the size of the Peru upwelling ecosystem

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Abstract

Previously published estimates of the area of the Peru upwelling ecosystem vary by more than an order of magnitude. In an effort to improve this situation, we used a 24-month sequence of SeaWiFS satellite images of chlorophyll in the surface water off Peru from 5°S to 18.5°S during September 1997–August 1999 to estimate the size of the nutrient enhanced productive habitat associated with the upwelling. The first 12-month period was marked by El Niño conditions, the second by strong upwelling. Using a chlorophyll threshold of \(>1.0\ \text{mg m}^{-3}\) to define the limit of the productive habitat resulted in maximum area estimates of \(120 \times 10^3\ \text{km}^2\) during September 1997–August 1998, and \(220 \times 10^3\ \text{km}^2\) during September 1998–August 1999. The latter result is consistent with an area estimate we calculated using total fishery landings and a regression relating fishery yields per unit area to annual primary production per unit area. Although year-to-year variation in the annual mean size of the upwelling ecosystem must be significant, even discounting El Niño events, our analysis has shown that at least five of the extreme earlier values are not good estimates of the size of the productive habitat. We may now be close to knowing the average size of the ecosystem to within a factor of about two. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The edges of marine ecosystems are often elusive. Perhaps, the most notorious example is the upwelling ecosystem off the coast of Peru (Mann and Lazier, 1996). Estimates of the size of this system range over ten-fold, from less than \(40 \times 10^3\ \text{km}^2\) to over \(500 \times 10^3\ \text{km}^2\) (Table 1). At least three factors contribute to this apparent uncertainty. First, some estimates refer only to the area of actual physical upwelling of water (e.g., Posner, 1957), while others include the larger area within which upwelled water and associated nutrients manifest a significant biological impact.

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Second, studies of the region have focused on different lengths of coastline (Table 1). Since one degree of latitude is equal to 110 km and the width of upwelling may range from about 270 km at 4°S to 60 km at 18°S (Chavez and Barber, 1987), the inclusion or exclusion of one degree near the equator might add or subtract about $30 \times 10^3$ km$^2$ from an estimate. Third, and probably most important, is the large seasonal and inter-annual variability in the extent of upwelling off Peru (e.g., Cushing, 1971; Feldman, 1986; Thomas et al., 1994), a characteristic of most upwelling systems (e.g., Strub et al., 1990).

Our purpose in this note is to apply two types of biological data to the task of estimating the size of the Peru upwelling ecosystem. The first data set consists of SeaWiFS satellite imagery of Chl $a$ concentrations in the surface water off Peru. The second consists of a large number of measurements obtained by others of primary production ($^{14}$C uptake) in the system (Chavez and Barber, 1987) as well as the fisheries landings for Peru recorded by the United Nations Food and Agricultural Organization (FAO).

### 2. Chlorophyll and the area of productive habitat

#### 2.1. Approach

Our approach follows the earlier effort of Feldman (1986), who first applied Coastal Zone Color Scanner satellite imagery to the problem of estimating the size of what he called the

<table>
<thead>
<tr>
<th>Source</th>
<th>Criteria</th>
<th>Latitude included</th>
<th>Area, 10$^3$ km$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Posner (1957)</td>
<td>Physical</td>
<td>3°S–14.5°S</td>
<td>21.4</td>
</tr>
<tr>
<td>Wyrtki (1963)$^a$</td>
<td>Physical</td>
<td>6°S–24°S</td>
<td>&lt;550</td>
</tr>
<tr>
<td>Wooster and Reid (1963)$^b$</td>
<td>Fisheries</td>
<td>~13.5° range</td>
<td>62</td>
</tr>
<tr>
<td>Ryther (1969)</td>
<td>Biological</td>
<td></td>
<td>36</td>
</tr>
<tr>
<td>Cushing (1971)$^c$</td>
<td>“Biological width”</td>
<td>~2°S–18.5°S</td>
<td>479</td>
</tr>
<tr>
<td>Feldman (1986)$^d$</td>
<td>1978–1979</td>
<td>Chl $a &gt; 1$ mg m$^{-3}$</td>
<td>5°N–15°S</td>
</tr>
<tr>
<td></td>
<td>1979–1980</td>
<td>Chl $a &gt; 1$ mg m$^{-3}$</td>
<td>5°N–15°S</td>
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<tr>
<td></td>
<td>1982–1983</td>
<td>Chl $a &gt; 1$ mg m$^{-3}$</td>
<td>5°N–15°S</td>
</tr>
<tr>
<td>Chavez and Barber (1987)</td>
<td>Physical</td>
<td>4°S–18°S</td>
<td>182</td>
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<tr>
<td>This study$^e$</td>
<td>1998–1999</td>
<td>Chl $a &gt; 1.0$ mg m$^{-3}$</td>
<td>5°S–18.5°S</td>
</tr>
<tr>
<td></td>
<td>1997–1998 (El Niño year)</td>
<td>Chl $a &gt; 1.0$ mg m$^{-3}$</td>
<td>5°S–18.5°S</td>
</tr>
</tbody>
</table>

$^a$“The entire area between 5°S and 15°S and as far as 500 km offshore is filled with Equatorial Subsurface water which is upwelling along the coast.”

$^b$“At least four million tons of anchovy can be removed in a year from the inshore water of Peru … a coastal strip less than 800 miles long and 30 miles wide.” This is about 75% of the coast of Peru.

$^c$The “biological width” was calculated as 2.5 times the width of physical upwelling. The area of physical upwelling used by Cushing was therefore 192,000 km$^2$.

$^d$Means for December and January only.

$^e$Based on 24 monthly composite images from September 1997–August 1999.
“productive habitat” associated with the Peru upwelling. Based on a limited amount of independent biological data, Feldman defined the productive habitat as the area in which surface water Chl $a$ concentrations exceeded 1 mg m$^{-3}$. Our analysis of the SeaWiFS imagery, however, also differed significantly from Feldman’s. He included the region from 5°N to 15°S and limited his analysis to the December and January period during three years (1978–1981, the last an El Niño year). We followed the more common practice of beginning at 5°S, near the Equator–Peru border (Table 1), and used monthly composite images over 24 months from September 1997 through August 1999. These monthly composites were formed from daily scenes remapped to a common grid with 4 km resolution. Since the first 12 months of our data record captured a strong El Niño event, we calculated annual mean areas for two 12-month periods, September 1997–August 1998 and September 1998–August 1999, using a range of chlorophyll values to define the nutrient enhanced productive habitat. For each chlorophyll level, (e.g., $>0.25$, $>0.5$, $>0.75$ mg m$^{-3}$, etc.) we summed the area of pixels from the coast to the most offshore pixel meeting the chlorophyll threshold concentration. We repeated this calculation at each 4 km band of latitude along the coast from 5°S to 18.5°S and then summed the result to give the total area of productive habitat. Visual inspection showed that chlorophyll concentrations declined in the seaward direction, and this approach minimized errors due to clouds or missing data that would have been problematic in a simple summation of all pixels with chlorophyll levels meeting the threshold criteria.

Fig. 1. Annual mean area of the upwelling ecosystem off Peru during the period September 1997–August 1998 (solid points) and September 1998–August 1999 (open circles) as a function of the threshold Chl $a$ concentration in surface water chosen to define the system. The 1997–1998 period was marked by a very strong El Niño.
2.2. Results

The choice of a threshold chlorophyll level defining the extent of “productive habitat” obviously has a great impact on the resulting area assigned to the upwelling ecosystem during both weak and strong upwelling years (Fig. 1). Assigning a specific value is admittedly arbitrary, but Feldman’s (1986) choice of >1 mg m\(^{-3}\) appears reasonable. Below this value, the area increases very rapidly as open ocean concentrations are approached, and above about 1 mg m\(^{-3}\) there is a relatively slow reduction in size as the chlorophyll threshold is increased. For example, reducing the chlorophyll threshold from 1.0 to 0.5 mg m\(^{-3}\) increases the area of productive habitat during a non-El Niño year by almost 120%, while increasing the threshold from 1.0 to 1.5 mg m\(^{-3}\) reduces the productive habitat area by less than 60%.

If we accept that the defining chlorophyll threshold lies at or above 1.0 mg m\(^{-3}\), the annual mean area of nutrient-enhanced productive habitat was less than 220 \times 10^3 \text{km}^2 during the period of strong upwelling (1998–1999) and less than 120 \times 10^3 \text{km}^2 during the year marked by a strong El Niño (Table 1). The mean size of the system during the El Niño year was thus about half of that during the La Niña year that followed. With a 1 mg Chl m\(^{-3}\) threshold, the size of the upwelling ecosystem varied monthly by almost nine-fold during the period of our analysis, from about 35 \times 10^3 \text{km}^2 in January of 1998 to 307 \times 10^3 \text{km}^2 in May of 1999 (Fig. 2). Coefficients of variation for the two 12-month periods were 44% and 32%, respectively.

3. Primary production and fisheries yield

3.1. Approach

The major reason for a long-standing and widespread interest in the Peru upwelling is the remarkable yield of fish, primarily anchoveta (*Engraulis ringens*), from the system. It therefore seemed instructive to see if the fisheries data are consistent with our estimates of productive habitat derived from the SeaWiFS chlorophyll imagery. Various authors have made theoretical calculations of the primary production required to sustain the total yield of fish (e.g., Ryther, 1969; Cushing, 1971), but it is possible to approach the problem from a more empirical perspective. Previous reviews have shown that there is a strong correlation between the rate of primary production per unit area and the yield of fish per unit area in a wide variety of marine ecosystems (Fig. 3) (Nixon, 1988; Iverson, 1990). Therefore, if the annual rate of primary production and the total fishery landings are known, it is possible to calculate the area of habitat supporting the fishery:

\[
\text{Productive habitat area} = \frac{\text{total landings}}{\text{calculated landings per unit area based on primary production}}
\]

3.2. Results

The most extensive recent effort to assess primary production in the Peru upwelling area concluded that carbon fixation from 4\(^{\circ}\)S to 16\(^{\circ}\)S averaged 2.28 g C m\(^{-2}\) d\(^{-1}\) or 835 g C m\(^{-2}\) yr\(^{-1}\) during 1983–1985, a period following the very strong El Niño of 1982 (Chavez and Barber, 1987). This is higher than systems previously included in the regression of fisheries yield as a function of primary production (Fig. 3), but extrapolation of the relationship suggests
Fig. 2. Area of surface water off Peru with Chl a concentrations > 1.0 and 0.5 mg m\(^{-3}\) during the period September 1997–August 1999 based on the analyses of composite monthly SeaWiFS images.

Fig. 3. The annual landings of fish and the primary production (\(^{14}\)C uptake) of phytoplankton in a wide variety of marine ecosystems. Measurements are often not contemporaneous. The regression analysis was performed on untransformed data. Systems include: (1) Southeast Mediterranean (post Aswan dam construction) (2) Bay of Bothnia (3) Open Gulf of Mexico–Caribbean (4) Sea of Okhotsk (5) Open Mediterranean (6) Adriatic Sea (7) Scotian Shelf (8) Sea of Japan (9) Bothnian Sea (10) Black Sea (11) Gulf of Finland (12) Gulf of Riga (13) English Channel (14) Baltic Sea proper (15) Corpus Christi Bay (16) Gardiners and Peconic Bays (17) North Sea (18) Gulf of Thailand (19) Mid Atlantic Shelf, US (20) Gulf of Maine (21) New England Shelf (22) Apalachicola Bay (23) Georges Bank (24) Great South Bay. Data sources in Nixon (1982) and Nixon et al. (1986). The relationship is discussed more fully in Nixon (1988).
that this level of primary production might support a fishery yielding 280 kg ha\(^{-1}\) yr\(^{-1}\). Unfortunately, Chavez and Barber’s (1987) study took place during a prolonged period of over a decade during which fishery landings from the Peru upwelling were very low as a result of El Niños in 1972 – 1973 and 1982–1983 and severe overfishing (FAO, 1997) (Fig. 4). Between 1983 and 1985, the landings averaged only 2.8 \(\times\) 10\(^6\) mt yr\(^{-1}\), whereas the upper quintile of landings since 1961 is about 10\(^7\) mt yr\(^{-1}\). If we accept the higher fisheries yield of 10\(^7\) mt yr\(^{-1}\) as more representative of production from the upwelling ecosystem when it is not experiencing El Niño conditions (or the consequences of severe overfishing), then Chavez and Barber’s (1987) primary production value leads to a calculated size of the productive habitat equal to some 360 \(\times\) 10\(^3\) km\(^2\), an area 1.6 times the upper estimate we calculated from the SeaWiFS imagery (Table 1).

However, Chavez and Barber (1987) noted that their measurements (made during a period when there were few fish in the system) were lower than the previous measurements and cautioned that, “...the mean productivity of the coastal region may be greater than 2.28 g C m\(^{-2}\) d\(^{-1}\) calculated for the 1983, 1984, and 1985 measurements”. The grand mean of the other studies they summarized came to 3.84 g C m\(^{-2}\) d\(^{-1}\) or 1400 g C m\(^{-2}\) yr\(^{-1}\). The relationship shown in Fig. 3 suggests that this level of primary production would support a fishery yield of 585 kg ha\(^{-1}\) yr\(^{-1}\), and combined with the total landings of 10\(^7\) mt yr\(^{-1}\), this would produce a productive habitat of 170 \(\times\) 10\(^3\) km\(^2\), an area equal to almost 80% of the size we calculated from the SeaWiFS imagery using the 1 mg chlorophyll m\(^{-3}\) threshold (Table 1). If primary production is about 1200 g C m\(^{-2}\) yr\(^{-1}\), the exercise yields an area of 210 \(\times\) 10\(^3\) km\(^2\), virtually the same as that based on chlorophyll. Given the uncertainty in the estimate of primary production, the large extrapolation applied to the primary production-fishery yield relationship, and the use of 1 mg m\(^{-3}\) as an upper estimate of the productive habitat definition, this seems a satisfying convergence. The result is also
roughly consistent with the distribution of the anchoveta, which Jordán (1971) describes as “…a typically coastal species encountered mainly within 50 miles of the coast and occasionally up to 100 miles out…” The area from 5°S to 18.5°S extending out 100 km from the coast is approximately $150 \times 10^3 \text{ km}^2$.

4. Conclusion—the size of the Peru upwelling ecosystem

The size of this system varies greatly through the year and from year-to-year (e.g., Fig. 2), but our goal has been to constrain the wide range in area estimates that have been reported (Table 1). Our results based on two independent approaches suggest that the trio of small ($<100 \times 10^3 \text{ km}^2$) estimates and the large values of Wyrtki (1963) and Cushing (1971) (Table 1) are not good descriptions of the productive habitat area. Feldman’s (1986) estimates applied only to December and January in each of three years and cannot fairly be compared with our annual means. Our averages for December and January using a $1 \text{ mgm}^{-3}$ chlorophyll threshold were $42 \times 10^3 \text{ km}^2$ in 1997–1998 and $195 \times 10^3 \text{ km}^2$ in 1998–1999. Our estimate for El Niño conditions is thus quite close to his, while our second year was about 60% smaller and 40% larger than his two comparable estimates (Table 1). The calculation of system size based on the physical data of Chavez and Barber (1987) is about 85% of the productive area resulting from a surface chlorophyll threshold of $1.0 \text{ mgm}^{-3}$. Considering that the area of nutrient-enhanced production should reasonably exceed that of physical upwelling, their estimate seems compatible with our results.

For non-El Niño conditions, we suggest that the mean annual area of the Peru upwelling ecosystem is about $220 \times 10^3 \text{ km}^2$ or less, based on the distribution of enhanced chlorophyll concentrations. If primary production in the upwelling during years with high fish yield ($\sim 10^7 \text{ mt yr}^{-1}$) is of the order of $1200 \text{ g C m}^{-2} \text{ yr}^{-1}$ or more, the relationship between primary production and fish yield per unit area from other, much less productive marine systems, provides habitat area estimates consistent with this conclusion. The spatial distribution of anchoveta, which provides over 90% of the landings from the upwelling system, also fits well within this framework. The coefficient of variation on this estimate over many years remains unknown, but it seems reasonable to assume that most of the variation during non-El Niño years will fall within the range $120–220 \times 10^3 \text{ km}^2$. We make this assumption because even the extreme El Niño of 1997–1998 only reduced the annual mean size of the productive habitat by about half, and 1998–1999 was a period of strong upwelling (Table 1). The two independent approaches we have used in this study appear consistent and have allowed us to reduce the apparent range in size from a factor of over 10 to a factor of less than 2.

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References


