

His¹⁷¹, and it is conceivable this serves the role of the missing His¹⁸. Finally, our studies suggest a means of improving the stability of hGH by including Zn²⁺ in pharmaceutical preparations and for engineering Zn²⁺ dimers of other helical hormones and proteins.

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Predictable Upwelling and the Shoreward Transport of Planktonic Larvae by Internal Tidal Bores

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Internal tidal bores have a crucial role in the transport of drifting larvae to marine nearshore populations, a key factor in structuring benthic communities. Shoreward transport of larvae and abrupt surface temperature drops lasting days can be explained by invoking the advection of subsurface cold water to the shore by internal tidal bores. This process is predictable within the lunar cycle and brings deep water to the surface (upwelling) in a direction perpendicular to the coastline.

KNOWLEDGE OF TRANSPORT MECHANISMS perpendicular to the coastline is essential to understanding the exchange of material and water properties between the nearshore and the coastal ocean; an important ecological example is the problem of the supply of pelagic larvae to intertidal and shallow habitats. The supply of recruits to benthic populations has long been recognized as a critical factor in structuring benthic communities (1). The rate at which planktonic larvae establish permanent contact with the substratum (settlement rate) (2) occasionally shows a wave form input. This pattern of settlement has been correlated with the onshore transport of barnacle and crab larvae by surface slicks generated by internal waves (3) and wind-induced currents (sometimes associated with synchronous offspring release) (4-6). Processes governing the transport of larvae are similar to those influencing the redistribution of water properties. Abrupt surface

water temperature drops during the summer in the Southern California Bight have been traditionally attributed to wind-driven Ekman upwelling (7, 8); however, most studies have been inferential (9), and there is only weak atmospheric forcing in the summer (10). Here it is proposed that the summer temperature drops visible in the Scripps Pier daily surface water temperature and the transport of planktonic larvae of nearshore organisms shoreward are both well explained by the advection of subsurface cold water (upwelling) resulting from predictable internal tidal bores.

In a manner similar to surface waves, internal waves change as they approach the shore. When wave amplitude becomes non-negligible with respect to water depth, the wave becomes asymmetrical; the leading edge steepens, the trailing edge flattens, and it propagates forward as an internal bore (11, 12). Internal waves (13, 14) and bores (12, 15) of tidal periodicity have frequently been observed in summer in the Southern California Bight. In fall and winter the water column within the Bight is typically weakly

stratified and internal motions are much less energetic (14, 16). A spring-neap surface tidal cycle suggests an internal tidal spring-neap cycle, as some claim to have observed (17). The internal tide, however, is not consistently in phase with the surface tide (13, 14). Passing internal waves produce vertical water displacements which can be recorded with fixed temperature sensors if the water column is thermally stratified. Thermal changes close to the bottom occurring in short time spans (on the order of 2° to 5°C over minutes) are salient features of internal bores and might indicate horizontal advection of water (figure 1 in 12, 15). Water temperature sensors were installed at two depths at the end of the Scripps Pier in August 1989. Large diurnal or semidiurnal fluctuations in bottom water temperature reveal internal tidal bores (Fig. 1). The hourly record shows that internal bores are ubiquitous in the summer, but they appear more infrequent in the fall portion of the record (Fig. 1A). Small-event internal bores are characterized by a layer of cold water restricted in its distance from the bottom (Fig. 1B, 5 August at about 3 a.m.). In the less frequent, large-event bores the cold water occurs from the bottom to the surface sensors (Fig. 1B, 8 August at about 2 p.m.; Fig. 1A, 20 to 24 August); in some cases, coinciding with the arrival of the bore, the surface temperature remains low for days (Fig. 1B); in others, lower and higher surface water temperatures occur alternately at apparently diurnal or semidiurnal periodicity without a persistent lowering of the surface temperature (Fig. 1A, 20 to 24 August). The data in Fig. 1 support the

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proposal that internal tidal bores might be responsible for the drops in surface water temperature. Surface water temperature has been recorded daily since about 1920 at the end of the Scripps Pier. Because only large-event bores influence surface waters, this historical record would only show some of the larger events.

The Scripps Pier historical temperature record has been used in testing the hypothesis that the coldest water temperatures oc-

cur during the spring tides because of tidal mixing; the hypothesis was refuted by Balch (18). However, he found that the daily temperature anomalies were nonrandomly distributed with respect to the lunar cycle; no further discussion was offered. Internal tidal bores could be an alternative explanation for the nonrandom distribution of the anomalies. The analysis (18) lumped all days of the year without regard to seasonal differences in stratification. Because internal

waves are most energetic if the water column is well stratified, the hypothesis that internal bores cause drops in surface water temperature predicts that partitioning the data into different seasons would show that the nonuniformity of the anomalies is highest in the season in which the water is most stratified. Each daily water-temperature anomaly (daily reading minus 1920 to 1988 day-of-the-year average) was fit to a lunar cycle day, partitioning the historical record into four calendar seasons. Figure 2 shows that in winter, when the water column is weakly stratified, the anomalies are uniformly distributed in the lunar cycle whereas in summer, with a well-developed stratification, the positive and negative anomalies tend to occur on different days of the lunar cycle; on average, the positive and negative anomalies are predictable within the lunar cycle (19). This supports the contention that internal tidal bores are responsible for the nonuniform distribution of the temperature anomalies and further supports the idea that internal tides are capable of lowering the surface water temperature for days.

Onshore transport processes are critical to coastal benthic populations and communities at several spatial and temporal scales; they influence the gene flow between disjunct populations, and they are the primary mechanism for replenishing nearshore populations after major disturbances. On a smaller scale, the supply of young planktonic individuals is a key factor in structuring many coastal benthic populations and communities (1, 2, 6, 20, 21). An important question, then, is what physical mechanism returns the planktonic larvae of species with complex life cycles to nearshore habitats.

The hypothesis that large-event internal bores return planktonic larvae of nearshore organisms from an undefined offshore larval reservoir predicts that peaks in nearshore larval abundance and settlement should coincide with the arrival of the largest events visible in the temperature record. Settlement plates were inspected daily for spat and cyprids of the cirripedes *Chthamalus spp.* and *Pollicipes polymerus* from 29 April to 8 August 1989 at Dyke Rock, a rocky shore located 500 m north of the Scripps Pier. There was a negative correlation between settlement and surface water temperature (Fig. 3); all correlation tests were statistically significant, and they appear better in late spring and summer than in early spring (22), supporting the idea that the mechanism which causes drops in water temperature is also transporting the larvae onshore.

The surface slick hypothesis (3) for the shoreward transport of larvae explicitly predicts that larvae should occur in surface

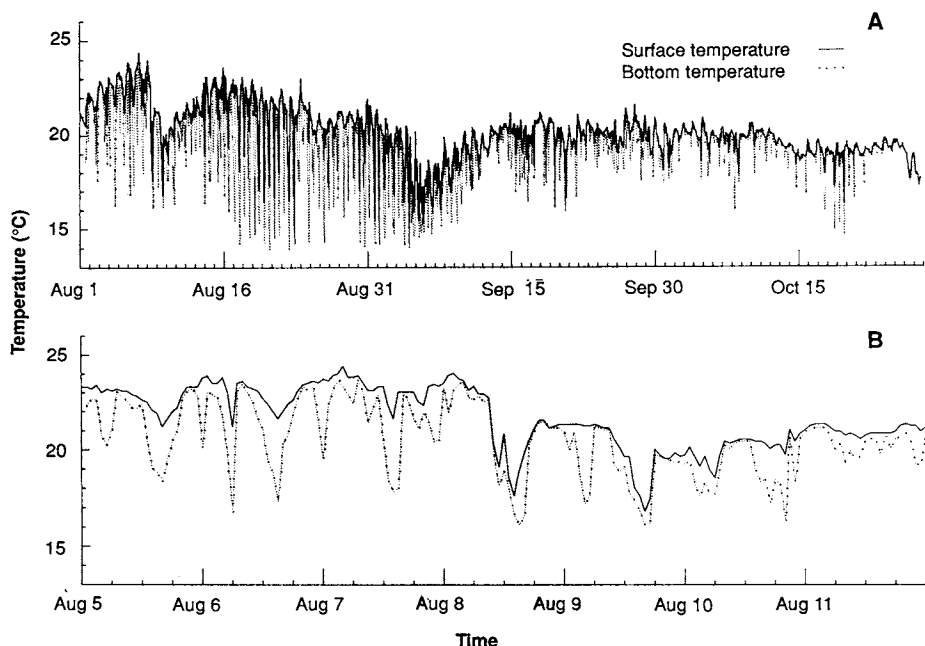


Fig. 1. Water temperature hourly record at the Scripps Pier automatic weather station (La Jolla, California) in 1989 at GMT. (B) is an expansion of (A). The "surface" sensor is located at about 0.5 m below the lowest water level and the "bottom" sensor at about 3 m below the surface sensor (1.5 m in average above the bottom).

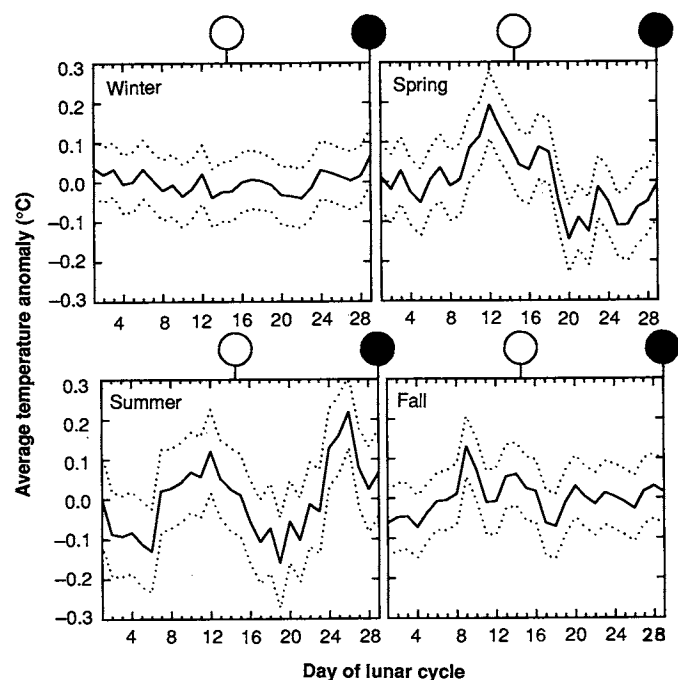


Fig. 2. Averaged water temperature anomaly (\pm SE, dotted lines) for each day of the lunar cycle ($n \approx 214$). Filled and hollow circles represent new moon and full moon. Anomalies were obtained from the Scripps Pier historical temperature record by subtracting the 1920 to 1988 day-of-the-year average from each daily reading (from 1920 to 1988; temperature is taken daily in the morning at surface waters at the end of the pier). The lunar cycle was divided into 29 units (days of lunar cycle; day 1 is one day after new moon). Each anomaly was then fit to a day of the lunar cycle (18) and to a calendar season.

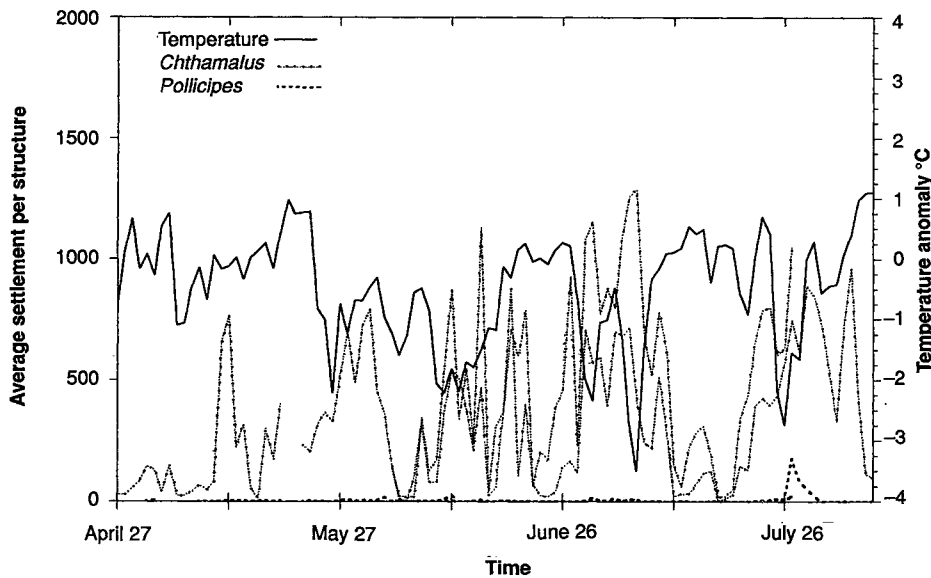


Fig. 3. Daily settlement rate for metamorphosed larvae plus attached cyprids of *Chthamalus* spp. and *Pollicipes polymerus* at Dyke Rock and daily water temperature anomaly (daily reading relative to the 1920 to 1988 day-of-the-year average) at the Scripps Pier in 1989. Two different dotted lines represent two different sites, separated by about 50 m. The broken dotted line in May represents missing data. Each curve shows the average of two to three grooved polyvinyl chloride settlement plates separated 0.5 to 2.0 m per site, including one or two horizontally oriented and one or two vertically oriented at about 0.75 to 1.50 m above mean lower low water level. The plates were replaced daily and inspected under the microscope. Only spat that settled in the angle between the base and the side of the groove were counted. Settlers strongly preferred corners. The total length of each settling plates' corners was 58.0 ± 0.4 cm (mean \pm SD, $n = 10$).

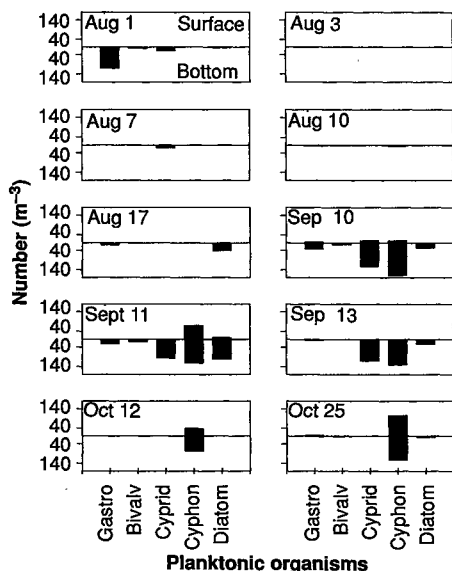


Fig. 4. Invertebrate larvae and centric diatom abundance at surface and bottom water depths. Each panel represents a single sampling date in 1990 in water sampled at the surface and at the bottom. Bottom samples were obtained by sampling at 0.5 to 1.5 m above the bottom while surface samples were taken by sampling the sea-air interface with a 200- μ m cod-end net. The water depth reached in the sea-air interface samples was about 0.02 m. Samples were taken by completing a 25-m transect parallel to the coastline two to four times at water depths ranging from 4 to 16 m in the vicinity of the Scripps Pier. Sample size ranged from 0.2 to 0.4 m^3 and from 0.1 to 0.2 m^3 for bottom and surface samples. Volume was calculated from transect distance covered and net-mouth area.

convergence zones; in a thermally stratified water column the larvae should occur at the surface in warm water. But if internal bores are transporting the larvae, they should be found in the cold water layer. Position within the water column, according to the internal bore hypothesis, is not that relevant if the water column is not well stratified because, on occasion, internal waves may overturn (23) or because the whole water column could be cold. The vertical center of distribution of barnacle cyprid larvae in a coastal locality near to Scripps was close to the bottom (24) and cyphonautes (bryozoan) larvae were more abundant at about 20 m depth than at the surface in the summer (21). This is true nearshore as well: invertebrate larvae and centric diatoms, a more passive indicator, were more abundant close to the bottom than at the surface (Fig. 4). Neither result supports the slick hypothesis for the surveyed organisms but, of course, it does not discard the possibility that surface slicks might transport the larvae of other species. Periodicity in settlement was interpreted as strong evidence for the surface slick hypothesis (3), but it is also consistent and better explained by the internal bore hypothesis. Since both phenomena require some water stratification, other mechanisms not considered here might transport the larvae in times or locations with a weakly stratified water column.

Ekman upwelling has been traditionally

invoked to explain drops in temperature in the Southern California Bight, but few measurements have been undertaken (9) and no alternative hypotheses were seriously considered. Here, a predictable mechanism that produces upwelling by advecting subsurface water to the shoaling nearshore is proposed that could be of great importance to nearshore ecological communities. Internal tidal bores well explain the drops in surface water temperature that have been correlated with increases in phytoplankton numbers and biomass (7, 25); internal tidal bores could be an important mechanism of nutrient supply. An understanding of such events is also important because of the possibility that contaminants deposited in some water layers could be transported back to shore. The Scripps Pier is in front of a submarine canyon that might intensify and direct internal waves. However, six out of nine coastal locations in California and one out of one in Washington revealed fortnightly variability at least as striking as that found for Scripps (Fig. 2) in summer (26). This suggests that the mechanism may be general and not a mere canyon effect. The surface slick hypothesis was put forth to explain the shoreward transport of planktonic larvae (3); after being tested and contrasted with an alternative, it is concluded that the internal tidal bore hypothesis better explains the phenomena for the surveyed organisms.

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A Component of Calcium-Activated Potassium Channels Encoded by the *Drosophila slo* Locus

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Calcium-activated potassium channels mediate many biologically important functions in electrically excitable cells. Despite recent progress in the molecular analysis of voltage-activated K^+ channels, Ca^{2+} -activated K^+ channels have not been similarly characterized. The *Drosophila slowpoke* (*slo*) locus, mutations of which specifically abolish a Ca^{2+} -activated K^+ current in muscles and neurons, provides an opportunity for molecular characterization of these channels. Genomic and complementary DNA clones from the *slo* locus were isolated and sequenced. The polypeptide predicted by *slo* is similar to voltage-activated K^+ channel polypeptides in discrete domains known to be essential for function. Thus, these results indicate that *slo* encodes a structural component of Ca^{2+} -activated K^+ channels.

POTASSIUM CHANNELS COMPRISE A large and diverse group of integral membrane proteins that determine the level of excitability and the repolarization properties of neurons and muscle fibers (1). On the basis of gating mechanisms K^+ channels can be subdivided into at least two distinct classes: voltage-activated K^+ channels respond to changes in membrane potential, whereas the gating of Ca^{2+} -activated K^+ channels is dependent on intracellular Ca^{2+} , although members of this class are also sensitive to voltage. Ca^{2+} -activated K^+ channels occur in neurons, muscles, and secretory cells of vertebrates and invertebrates and govern action potential repolarization, the rate and pattern of repetitive firing, and Ca^{2+} entry (2).

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The molecular analysis of K^+ channels was initiated by the cloning of the *Drosophila Shaker* (*Sh*) locus, a gene encoding one class of voltage-activated K^+ channels (3). Subsequently, many K^+ channel genes were cloned from various organisms on the basis of sequence similarity with *Sh*, enabling elucidation of important structural features essential to K^+ channel activity (4). However, none of these genes appears to encode a K^+ channel gated by Ca^{2+} .

In *Drosophila*, a fast, Ca^{2+} -activated K^+ current, I_{CF} , has been identified in adult and larval muscles and in larval neurons (5-7). Like the BK class of Ca^{2+} -activated K^+ channels in mammalian muscle (8), the *Drosophila* channels that conduct I_{CF} are sensitive to charybdotoxin and have a relatively large single channel conductance (6, 7). Mutations of the *slo* locus specifically eliminate I_{CF} (6, 7, 9). To determine if *slo* encodes a structural component of Ca^{2+} -activated K^+ channels or perhaps affects

their function by some other means, we undertook a molecular analysis of this locus (10).

We first pinpointed the cytological location of the gene, defined on the basis of a single, cytologically normal mutation, *slo*¹ (6). We mapped this mutation by meiotic recombination to position 90.0 on the third chromosome between *bar-3* (map position 79.1) and *taxi* (map position 91), corresponding to polytene chromosome region 95-96 (11). To refine this location, we isolated three γ -ray induced *slo* mutations (*slo*³, *slo*⁴, and *slo*⁸) on the basis of their failure to complement the *slo*¹ behavioral phenotype (6, 12) (Table 1). The *slo* phenotype of these new mutations was confirmed electrophysiologically (13).

Cytological examination of these mutations revealed that all contained chromosome rearrangements with a common breakpoint at polytene band 96A17 (Table 1). These results together with the cytological and genetic characterization of other chromosome lesions in this region, originally isolated by other criteria, identify band 96A17 as the cytological location of *slo* (Table 1).

One of the breakpoints in the *slo*⁴ inversion is at the *slo* locus and the other is at 96F5-8 close to the previously cloned *E(spl)* locus (14). We were thus able to use this inversion to clone genomic DNA from the *slo* locus by chromosome walking and jumping (15). Chromosomal in situ hybridization of two sets of phage clones from existing chromosome walks in the *E(spl)* region revealed that one set was proximal and the other set distal to the 96F5-8 breakpoint. Consequently, we extended the proximal walk by isolating overlapping cosmids from a wild-type library until the 96F5-8 breakpoint was reached. To identify a cosmid spanning the inversion breakpoint (Fig. 1A), we assayed each cosmid from the walk

Table 1. Summary of chromosome aberrations used in cytological mapping of the *slo* locus.

| Name | Cytological lesion | <i>slo</i> phenotype |
|-------------------------|------------------------------------|----------------------|
| <i>slo</i> ¹ | Normal | Mutant |
| <i>slo</i> ³ | Deletion (95E6-7 to 96A18) | Mutant |
| <i>slo</i> ⁴ | Inversion (96A17 and 96F5-8) | Mutant |
| <i>slo</i> ⁸ | Deletion (96A2-9 to 96D2-4) | Mutant |
| <i>Df(3R)S87-5</i> | Deletion (95F7-9 to 96A17-18) | Mutant |
| <i>Df(3R)S87-4</i> | Deletion (95E8-F1 to 95F15-96A2) | Normal |
| <i>T(Y;3)A117</i> | Translocation (broken at 96A10-17) | Mutant |