ELSEVIER

Water Research 39 (2005) 3565–3578

WATER RESEARCH

www.elsevier.com/locate/watres

An analytical model of enterococci inactivation, grazing, and transport in the surf zone of a marine beach

Alexandria B. Boehm[a,*], Daniel P. Keymer[a], Gregory G. Shellenbarger[b]

[a]*Department of Civil and Environmental Engineering, Environmental and Water Studies, Stanford University, Stanford, CA 94305-4020, USA*

[b]*401 13th Street, Sacramento, CA 95814, USA*

Received 28 September 2004; received in revised form 28 March 2005; accepted 27 June 2005

Abstract

An analytical model of enterococci (ENT) concentrations in the surf zone of a long sandy beach is constructed considering the physical processes of dilution by rip currents and alongshore littoral drift, and the biological processes of inactivation and mortality by grazing. The solution is used to construct an expression for the length of shoreline adversely impacted by ENT from a point source. Two non-dimensional parameters are developed whose magnitude can be used to ascertain whether dilution, inactivation, or grazing is the dominant sink for ENT in the surf zone. The model is applied to beaches in southern California, USA. Model input parameters related to physical processes and inactivation are compiled from the literature. Laboratory experiments are conducted to determine grazing mortality rates of ENT ($6.5 \times 10^{-6}\,\mathrm{s}^{-1}$). Results indicate that at the field sites, between 1000 and 5000 m of shoreline are typically impacted by a continuous point source of ENT. Dilution is the primary cause of decline in ENT concentrations within the surf zone, with inactivation secondary and grazing tertiary. Results recommend strategic positioning of point sources and timing of effluent releases to take advantage of high dilution conditions. Our estimates for grazing mortality rates are within the same order of magnitude as some published inactivation rates, thus we cannot rule out the possibility that grazing is an important sink for ENT, especially in low dilution environments like enclosed bays.

Keywords: Bacterivory; Grazing; Surf zone transport; Inactivation; Enterococci

---

1. Introduction

Enterococci (ENT) are presently the best metric for assessing risk of illness associated with recreating in marine waters (Wade et al., 2003). ENT pollution in marine waters is of great concern to coastal communities because of potential increases in illness rates amongst swimmers. In addition, beaches represent a source of revenue and have significant non-market values (Rabinovici et al., 2004). Efforts to identify and remedy ENT contamination has proven difficult because little is understood about the transport and extra-enteric ecology of the organisms. This, in turn, limits projection and modeling of how point or non-point sources of ENT will adversely impact coastlines.

After released into the marine environment from a point or non-point source, ENT concentrations may decrease due to transport (advection and dispersion), inactivation, and removal. There is little evidence that these organisms reproduce in seawater, although some work suggests their proliferation in marine sediments

---

[*] Corresponding author. Tel.: 650 724 9128; fax: 650 725 3164.
E-mail address: aboehm@stanford.edu (A.B. Boehm).

doi:10.1016/j.watres.2005.06.026

(Desmarais et al., 2002). Transport rates depend on ocean currents and turbulence, which in turn are forced by tides, breaking waves, winds, and other oceanic phenomena. Dominant transport mechanisms vary with location in the marine environment. ENT senescence and death, hereafter referred to as "inactivation", occur when bacteria undergo mutation, lysis, dwarfing, or oxidative-damage due to environmental stress (Nystrom, 2004). Temperature, salinity, sunlight, and lack of nutrients contribute to inactivation of ENT in natural waters (e.g., Noble et al., 2004; Hanes and Fragala, 1967; Boehm et al., 2002). Removal from the water column may be physically or biologically mediated. Physically mediated removal occurs via interaction with sorbents such as particles/sediments, and subsequent sedimentation. While ENT have been found at high levels in sediments (Desmarais et al., 2002), the mechanisms of ENT sorption and sedimentation have not been studied extensively in marine waters. Biologically mediated removal of ENT occurs via predation by bacterivorous protozoa (e.g., amoebas, forams, nanoflagellates and ciliates) and various other zooplankton (hereafter, collectively referred to as grazers) (McCambridge and McMeekin, 1981; Barcina et al., 1997; Hartke et al., 2002; Menon et al., 2003). An additional possible biological removal mechanism for ENT in marine waters is infection by lytic bacteriophage; however, to our knowledge, this removal mechanism has not been thoroughly evaluated in marine waters.

The goal of the present study is to develop an analytical model for the alongshore distribution of ENT in the surf zone that considers the physical processes of alongshore advection and rip-current mediated dilution, and the biological processes of inactivation and removal due to grazing. These processes are chosen for the analysis because they have been extensively documented in marine waters. The implications of not including other removal mechanisms such as physically mediated removal and infection by lytic phage in our analysis will be discussed. The model is used to develop an expression for the length of shoreline adversely impacted by a continuous point source of ENT to the surf zone. In addition, two non-dimensional parameters are formulated, the values of which allow one to resolve the relative importance of inactivation, grazing, and dilution in controlling the distribution of ENT along the shoreline. The model is applied to a field site in Huntington Beach (HB), California using parameters from published studies and laboratory experiments to determine which process is dominant in controlling ENT concentrations along the shoreline away from hypothetical point sources.

2. Model development

For the purposes of this study, the surf zone is defined as the region of the coastal zone between where waves begin to break and the shoreline (Fig. 1). Detailed field work (Inman et al., 1971) has revealed that when conservative material is introduced to the surf zone, it undergoes rapid mixing across the width and depth of the surf zone due to wave-driven turbulence, followed by transport parallel to the shore by wave-driven longshore currents, and dilution by rip cell exchange of ocean water between the surf zone and offshore. The

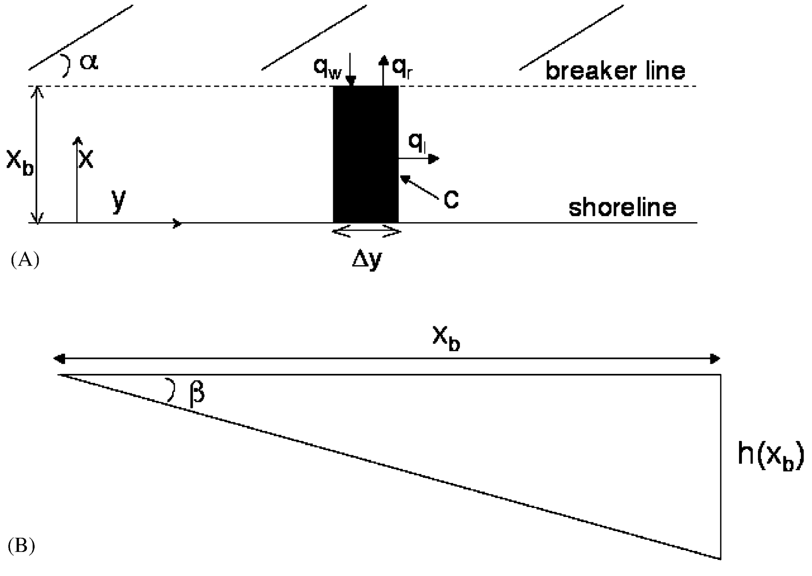

Fig. 1. Panel A. Top view of surf zone with variables used in model. Panel B. Profile view showing triangular cross section with slope $S = \tan\beta$. See text for descriptions of variables. The z direction is not illustrated, but describes the dimension into the page of Panel A.

depth-averaged longshore transport velocity q_l can be estimated from the wave angle of attack upon the shoreline α, the slope of the beach S, and the height of the breakers h_b (in meters) using the Longuet-Higgens equation (Longuet-Higgens, 1970a, b):

$$q_l = 20.7S\sqrt{gh_b}\sin\alpha\cos\alpha, \tag{1}$$

where g represents the gravitational acceleration constant and q_l is in m s^{-1}. The cross-shelf velocities q_w and q_r in Fig. 1 describe the depth-averaged velocities of water entering the surf zone over the top of breaking waves and exiting the surf zone through rip-currents in the x-direction, respectively. To our knowledge, there are no theoretical expressions for these velocities.

Inman et al. (1971) and Inman and Brush (1973) described the transport of a conservative suspended pollutant in the surf zone. Using a "tanks-in-series" model, they showed that the concentration of pollutant a distance y alongshore from a steady point source at $y = 0$ is

$$C = C_0(R_l)^{y/Y}, \tag{2}$$

where C_0 is concentration of the pollutant in the surf zone adjacent to the point source, Y is the rip cell spacing, and R_l, which varies from 0 to 1, characterizes the dilution that occurs over a single rip cell due to offshore exchange with ocean water ($R_l = 0$ corresponds to complete dilution and $R_l = 1$ corresponds to no dilution). This solution is for the case where water outside the surf zone contains no contaminant. Eq. (2) predicts the exponential decay of pollutant concentration along the shoreline. This is, in general, in agreement with field observations of dye released from a continuous point source to the surf zone (Inman et al., 1971; Grant et al., 2000). Thus, despite the complex hydrodynamics in and near the surf zone, the simple box model employed by Inman et al. (1971) appears to account fairly well for the physics of surf zone transport.

In previous work examining ENT in the surf zone of HB, California (Grant et al., 2001; Boehm et al., 2002), we noticed that ENT appeared to decline exponentially in the direction of littoral drift away from ENT point sources. While this decay might be explained by dilution of ENT-laden surf zone water with ENT-free ocean water, it might also be explained by the first-order decay or removal of ENT due to inactivation or grazing as the water moves alongshore at a constant velocity q_l with no dilution. In order to understand the conditions under which grazing, inactivation, or dilution may dominate the alongshore attenuation of ENT, the Inman et al. (1971) model described above was modified to account for the non-conservative behavior of ENT. It is assumed that non-conservative behavior is due to (1) the first-order decay of ENT due to inactivation which has been studied extensively, and (2) grazing by bacterivorous organisms. In constructing this model, we have ignored potential removal mechanisms such as adsorption to sediment and subsequent sedimentation or deposition on the shoreline, and infection by lytic phage. The importance of these processes on ENT fate has not, to our knowledge, been thoroughly documented in marine waters. We will discuss the implications of not including these removal terms in the results section.

A mass balance over an elemental length of fluid in the surf zone (Fig. 1) yields the following differential equation:

$$\frac{\partial C}{\partial t} = -q_l\frac{\partial C}{\partial y} - \left(\frac{2q_r}{x_b} + k + g\right)C, \tag{3}$$

where $C(y,t)$ is the concentration of ENT, x_b is the width of the surf zone measured from the shoreline to the edge of the breaker zone, k is the inactivation rate constant, g is the grazing rate, q_r and q_l are as defined previously, and t and y are time and distance along the shore, respectively. In formulating Eq. (3), the following assumptions have been made: (1) the surf zone is well mixed in the x and z directions, (2) the cross-sectional area of the surf zone is triangular in shape with a constant slope, (3) both onshore flux of clean water and offshore flux of polluted water occurs intermittently (in time) at the offshore boundary of the surf zone, (4) there are no regional gradients in the flow field (i.e., $q_w = q_r$), (5) there is no accumulation of the pollutant outside the surf zone (i.e., no pollutant enters via q_w), (6) q_r and q_l are constant with respect to y, and (7) turbulent dispersion is not significant compared to advection in the y direction. Most of these assumptions are discussed in detail by Inman et al. (1971). Assumption 3 is tantamount to assuming that ejection of water accumulated in the surf zone due to breaking waves is not isolated to rip currents, but occurs along the entire surf zone (i.e., the tank-in-series model of Inman et al. (1971) is changed to a plug flow reactor). A similar assumption was made by Cheng et al. (2000) for modeling the transport of oil in the surf zone. Assumption 3 should not affect the results presented here so long as y is greater than rip cell spacing. In light of these simplifying assumptions, Eq. (3) should be regarded as a first-order approximation of a highly complex system that is not completely understood. Nevertheless, as mentioned earlier, such a conceptualization of surf zone transport has proven successful at capturing the fundamental behavior of conservative pollutants (Inman et al., 1971).

For the steady-state case where the pollutant point source is continuous, the solution of Eq. (3) suggests that the concentration of a contaminant away from its source decays as an exponential with distance from the source:

$$\ln(C/C_0) = -\frac{y}{l_{\mathrm{eff}}} \tag{4a}$$

with

$$l_{\mathrm{eff}} = \frac{1}{1/l_{\mathrm{dil}} + 1/l_{\mathrm{die}} + 1/l_{\mathrm{graz}}}, \tag{4b}$$

$$l_{\mathrm{dil}} = \frac{q_l x_b}{2q_r}, \quad l_{\mathrm{die}} = q_l/k \quad \text{and} \quad l_{\mathrm{graz}} = q_l/g, \tag{4c}$$

where l_{dil}, l_{die}, and l_{graz} physically represent the longshore distances over which ENT levels decrease to $1/e$ their values at $y = 0$ (e.g., C_0) due to cross shore mediated exchange of surf zone and offshore ocean water, inactivation, and grazing by bacterivorous organisms, respectively. Based on Eqs. (4b) and (4c), the length of shoreline impacted by ENT pollution depends on the coastal morphology, wave climate, inactivation of ENT, and grazing of ENT in the particular environment under study. Eq. (4b) can be utilized to predict the length of coastline that will be impacted by a point source, provided that approximations can be made for l_{dil}, l_{die}, and l_{graz}.

Of the three parameters, l_{dil} is the most difficult to estimate because of the uncertainty involved in predicting q_r. l_{dil} can also be expressed in terms of the dilution factor R_l and rip cell spacing Y: $l_{\mathrm{dil}} = -Y(\ln R_l)^{-1}$. Inman et al. (1971) give estimates for R_l as a function of α. The ratio of q_l/q_r in Eq. (4c) can also be conceptualized as a measure of dilution. When waves break perpendicular to the coast line ($\alpha = 0°$), $q_l/q_r \approx 0$, and there is complete dilution. Dilution decreases (q_l/q_r increases) as α increases and waves attack the shoreline at a more oblique angle.

The parameters l_{die}, l_{graz}, and l_{eff} can be readily quantified given alongshore concentrations of ENT away from a point source, laboratory measurements of k and g, and field records of wave angle and direction. These parameters alone can be used to gain insight into the importance of biological (inactivation and grazing) and physical processes (dilution) in controlling the attenuation of ENT up- or downcoast of a point source to the surf zone. The relative importance of inactivation, grazing, and dilution is reflected in the magnitude of two-dimensionless parameters:

$$\Gamma = \frac{l_{\mathrm{eff}}}{l_{\mathrm{die}}} = \frac{1/l_{\mathrm{die}}}{1/l_{\mathrm{dil}} + 1/l_{\mathrm{die}}}, \tag{5a}$$

$$\Phi = \frac{l_{\mathrm{eff}}}{l_{\mathrm{graz}}} = \frac{1/l_{\mathrm{graz}}}{1/l_{\mathrm{dil}} + 1/l_{\mathrm{graz}}} \tag{5b}$$

which range from 0 to 1.

Fig. 2 illustrates the ratio $l_{\mathrm{eff}}/l_{\mathrm{dil}}$ as a function of Φ and Γ based on the following relationship:

$$\frac{l_{\mathrm{eff}}}{l_{\mathrm{dil}}} = 1 - \Gamma - \Phi. \tag{6}$$

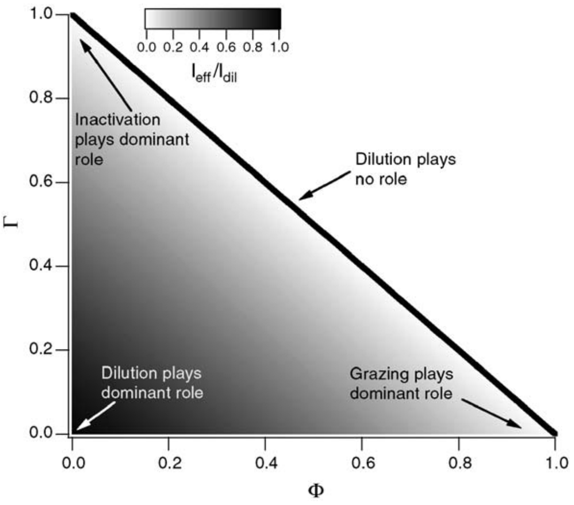

Fig. 2. The parameter space of the model of dilution, inactivation, and zooplankton grazing of ENT in the surf zone of a long, sandy beach. See text for definitions of Γ and Φ.

Since l_{eff} cannot be greater than any of the three length scales l_{dil}, l_{die}, and l_{graz}, regions of the graph beyond the axes and the line $\Gamma = 1 - \Phi$ are not within the parameter space of the model. Each vertex of the triangle represents the condition where one process dominates the attenuation of ENT alongshore. In the limit that $\Gamma = \Phi \to 0$, dilution is dominant. In the limit $\Gamma \to 1$, inactivation is dominant, while as $\Phi \to 1$, grazing is dominant. Along the sides of the triangle, one of the three processes can be ignored and classified as unimportant. As illustrated in Fig. 2, the hypotenuse delineates conditions under which dilution is unimportant. Along the line representing $\Gamma = 0$, inactivation is unimportant. Finally, along the line $\Phi = 0$, grazing is not important.

In a previous study, we examined the behavior of a system along the line $\Phi = 0$ (Boehm, 2003). Specifically, we examined how the biological process of inactivation and the physical process of dilution interact to control fecal indicator bacteria along the shoreline of a long sandy beach. We then applied the model to total coliform levels in the surf zone of Huntington and Newport Beach, California. Based on the values of Γ at these beaches, we determined that, in general, inactivation played a minor role in the alongshore attenuation of total coliform from a point source relative to dilution.

In the current study, we determine how the removal process of grazing influences the alongshore attenuation of ENT relative to inactivation and dilution at a subset of beaches in southern California. The goal is to determine the length of shoreline adversely impacted by a momentumless point source of ENT (l_{eff}) and examine the magnitudes of Γ and Φ in order to determine under what environmental conditions grazing needs to be considered in the modeling of ENT levels in the surf zone. This requires the determination of g (mortality rate by grazing) in the marine surf zone of California beaches.

3. Model application

3.1. Field site

To illustrate an application of the model, we examine the fate of ENT released from theoretical momentumless point sources during typical dry weather conditions (June, July, and August—JJA) along the wave-energy dominated coast of Huntington and Newport Beach, California, USA (Fig. 3). The field site consists of beaches that face slightly different directions. Our analyses will focus on northern beaches with shorelines oriented 125/305° from true north (located between white arrows in Fig. 3), and southern beaches oriented 111/291° from true north (located between black arrows in Fig. 3), hereafter referred to as N beaches and S beaches, respectively. The region between these sets of beaches is omitted from the study because groins are spaced along the shoreline to prevent erosion, and these undoubtedly influence alongshore transport and dilution. Dilution is enhanced about such structures due to permanent rip currents that develop on the wave exposed sides. The transport between and around the groins cannot be modeled using the simple analytical tools described above.

3.2. Materials and methods

3.2.1. Marine observations and q_1

The HB Lifeguards record surf direction and size three times per day (at approximately 7:00, 13:00, and 17:00 h). Measurements are made visually by experienced individuals (trained lifeguards) familiar with the beaches. Wave direction, to the nearest 10°, is reported relative to magnetic north; breaker height as a range of minimum to maximum. In this region, magnetic north is offset approximately 14° to the east of true north. Records from 1990 through 2001 were used to estimate seasonal wave climates for the dry weather season (JJA) and to calculate littoral currents using Eq. (1). In our analysis, we have assumed that the wave conditions reported at HB apply equally well to beaches along the entire study area, a sensible assumption given the close proximity of the beaches (all within 12 km). In addition, observations at Newport and HB by local coastal science experts and lifeguards over many years corroborate this assumption (David Pryor, Associate California State Park Resource Ecologist, personal communication, September, 2003).

The prevailing wave climate (both direction and height) during JJA is summarized in Boehm (2003) and reproduced in Table 1, along with the angle at which the waves impinge upon the shorelines at N and S beaches (α in Eq. (1)) and the direction of resulting littoral drift. Averages and standard deviations of wave height and frequency of occurrence were calculated by comparing values for each of the 11 years. Based on the standard deviations, there is not a large year-to-year variation in wave climate. Although supra-decadal

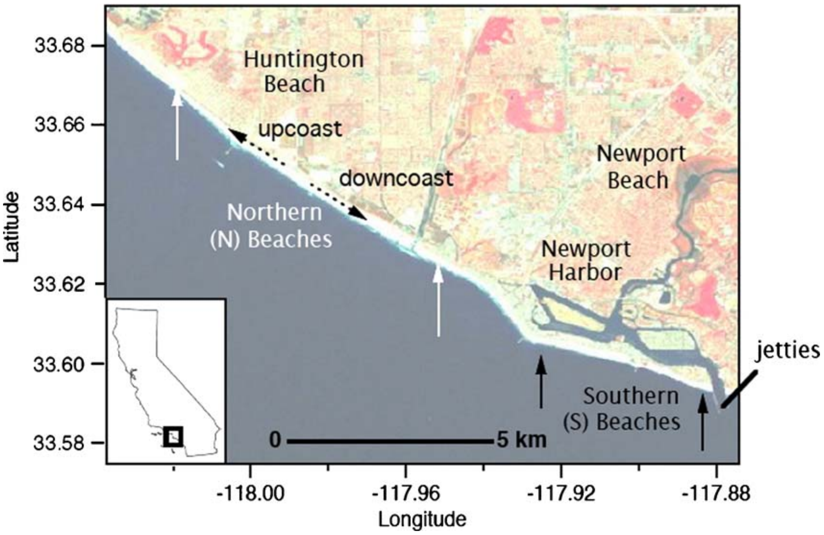

Fig. 3. Map of field site (courtesy USGS seamless database). Northern (N) beaches are those between white arrows. Southern (S) beaches are those between black arrows. The Newport Harbor jetties are highlighted, as are our definitions of up- and downcoast (dashed arrows).

Table 1
The average wave climates during the summer months of JJA as estimated from marine observations recorded from 1990 through 2001 by the Huntington Beach Lifeguards

Wave direction from	% of total observations	Average height (m)	α, angle of attack at N beaches	α, angle of attack at S beaches
W	4 ± 3	0.52 ± 0.08	67°D	82°D
WSW	11 ± 7	0.57 ± 0.08	44.5°D	59.5°D
SW	45 ± 8	0.59 ± 0.09	22°D	37°D
SSW	21 ± 5	0.68 ± 0.10	0.5°U	14.5°D
S	19 ± 10	0.77 ± 0.10	23°U	8°U

Errors describe inter-annual variations in wave climates and were obtained by calculating percents and average heights for JJA of each year and then computing the standard deviations. The angle of attack of waves from a specified direction upon the shoreline at N and S beaches and the resulting direction of littoral drift (U ≡ upcoast, D ≡ downcoast) were calculated using the strike of the coastline as 125/305° and 111/291° from true north, for N and S beaches, respectively. Upcoast is defined as to the northwest, downcoast as to the southeast (see Fig. 3). This table updates several inconsistencies in Boehm (2003).

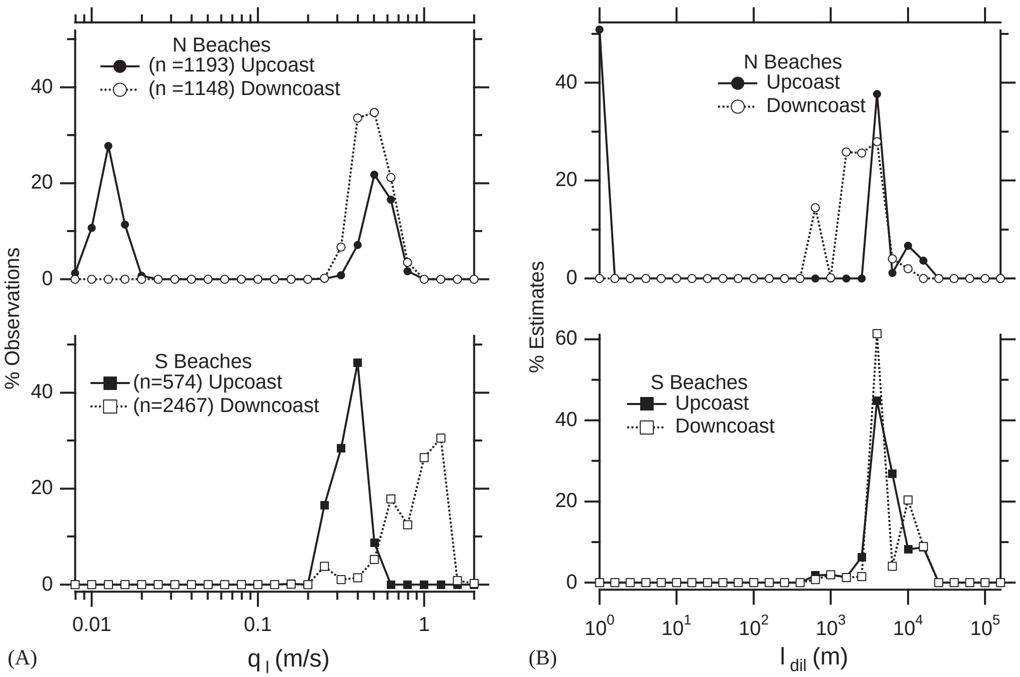

Fig. 4. Frequency distributions of q_l (panel A) and l_{dil} (panel B) taken from Boehm (2003) for N (circles) and S (squares) beaches during upcoast (filled symbols) and downcoast (open symbols) littoral drift. The frequency with which values are observed for each bin is denoted by a marker placed at the highest end of each bin.

oscillations in atmospheric and oceanic conditions that might affect the wave climate are not captured by the 11 year time series of wave conditions, it is reasonable to assume that the wave climate is typical of dry weather conditions, especially given the year-to-year similarities in wave conditions.

Waves emanate from the south and southwest approximately 64% of the time, with the largest waves, on average, arriving from the south. JJA waves can generate up- and downcoast littoral drift at both N and S beaches. Hence, pollution from a point source can be advected in up- or downcoast directions, depending on the direction of the impinging waves.

Fig. 4 Panel A shows frequency distributions of q_l for both beaches (labeled N and S), taken from Boehm (2003). Solid and dotted lines represent q_l directed in the up- and downcoast directions, respectively. The number of marine observations utilized to obtain each frequency distribution is given in the figure. At N beaches, q_l directed up- and downcoast are distributed log-normally about 0.5–0.6 $\mathrm{m\,s^{-1}}$. The upcoast directed q_l have a secondary peak centered about 0.013–0.016 $\mathrm{m\,s^{-1}}$, representing about 50% of the upcoast directed estimates. These small q_l result during waves from the south-southwest for which $\alpha \approx 0$ (Table 1). At S beaches, upcoast littoral currents are log-normally distributed about $0.4-0.5\,\mathrm{m\,s^{-1}}$ with 100% of the estimates between 0.2 and 0.6 $\mathrm{m\,s^{-1}}$. The downcoast currents are spread over a wider range of values from 0.1 to 2 $\mathrm{m\,s^{-1}}$. The highest frequency of currents occurs in 0.6–1.6 $\mathrm{m\,s^{-1}}$ range (87%). Dye experiments conducted at HB during southerly waves revealed upcoast littoral speeds of about 0.5 $\mathrm{m\,s^{-1}}$ (Grant et al., 2001), indicating the predictions made here are within the range of field observations.

3.2.2. Length scale for dilution l_{dil}

l_{dil} for N and S beaches were estimated previously by Boehm (2003) at the field site (Fig. 4 Panel B). The estimates were made using alongshore distributions of total coliform near point sources, assuming that inactivation and dilution were the main processes impacting total coliform fate. The estimates represent a lower bound for l_{dil}, since other removal processes may be important. l_{dil} is independent of the pollutant under study, but depends on the field site's coastal morphology, including beach slope, orientation, and wave climate. Ideally, extensive field data should be used to estimate l_{dil} (for example, Inman et al., 1971); however, such data are available for only a few beaches around the world under a limited number of wave conditions. Given the limitations in data availability, these l_{dil} serve as a reasonable starting point for attempting to understand the factors that control ENT distributions along wave-exposed sandy shorelines. The use of these distributions will be discussed in the results and discussion section.

Fig. 4 Panel B shows up- and downcoast l_{dil} for N and S beaches. At N beaches, l_{dil} ranges from 0 to 4000 m, and 1000 to 4000 m when waves produce up- and downcoast littoral drift, respectively. The small length scales in the upcoast direction (<1000 m) arise during waves from the south-southwest (with small α) that minimize alongshore transport and promote rapid flushing of rip cells to offshore waters (Inman et al., 1971). Assuming a rip cell spacing of 500 m (Boehm, 2003), this implies that during south swells, *e*-fold reduction in conservative pollutant levels from a momentumless point source due to dilution occurs over approximately 4–8 rip cells. During west, southwest, and west-southwest wave conditions, similar pollutant dilution occurs over 1–8 rip cells, depending on wave height and the exact direction of the waves. The greatest dilution length scales likely occur during westerly waves when the angle of attack is the largest.

At S beaches, up- and downcoast dilution length scales share similar distributions. The majority of l_{dil} are between 2000 and 4000 m, indicating that dilution mediated *e*-fold reductions in pollutant levels occurs primarily over 4–8 rip cells (assuming $Y = 500$ m as above). This result should be interpreted cautiously for downcoast l_{dil} because the model does not explicitly consider dilution caused by the harbor jetty, located at the southern end of the S beaches, on the north side of the Newport Harbor entrance (Fig. 3). If a point source is present within 4–8 rip cells of the jetty, then the length scale over which dilution alone would cause decline in pollution is probably significantly smaller than 4–8 rip cells because jetties induce strong rip currents on their wave exposed side (Rijn, 1998).

3.2.3. Estimation of l_{die}

The length scale along the beach over which ENT are attenuated due to inactivation alone (l_{die}) was estimated as follows. The littoral current q_l (speed and direction) estimates shown in Fig. 4 Panel A were placed into logarithmically spaced bins to construct cumulative distribution functions (CDFs).

Die-off rates (k) were compiled from the literature on inactivation of ENT in natural waters (Table 2). The inactivation experiments represented in Table 2 were conducted with waters and sediments with varying chemistries and microbial communities, and this may explain the differences in ENT inactivation rates reported. There is also evidence that the stress history of an allochthonous bacterium may affect its inactivation rate (Gauthier et al., 1992). The differences in natural water characteristics and initial stress levels of seed organisms have not been accounted for in our treatment of these values from the literature. Rather, we consider these experimental values as one-time realizations of a complex process that can be best represented by a distribution function. Thus, the information in Table 2 was compiled into a CDF for use in our model. While perhaps not a perfect representation of the complex distribution of ENT inactivation rates pertinent to the surf zone, the frequency distribution serves as a reasonable starting point for the model.

l_{die} were calculated by randomly sampling q_l and k CDFs 10,000 times, and taking the quotient. These were subsequently divided into logarithmically spaced intervals and displayed as frequency distributions representing typical l_{die} for N and S beaches during up- and downcoast littoral currents.

3.2.4. Estimation of l_{graz}

The length scale along the beach over which ENT are attenuated due to grazing alone (l_{graz}) was estimated using q_l distributions described above and g calculated from two laboratory experiments. The g values from the experiments were averaged and used as the divisor in the quotient q_l/g that represents l_{graz}. The resulting estimates of l_{graz} were divided into logarithmically spaced intervals and displayed as frequency distributions representing typical l_{graz} for N and S beaches.

Table 2
Compilation of ENT inactivation rates from the literature

k (s^{-1})	Description	Reference
4.0×10^{-6}	Belgian coastal waters	(Menon et al., 2003)
2.7×10^{-6}	Storm drain sediment[1]	
1.4×10^{-6}	Seawater, cold, dark	(Sinton et al., 1994)
2.2×10^{-6}	Seawater, warm, dark	(Sinton et al., 1994)
2.2×10^{-6}	Seawater, cold, dark	(Sinton et al., 1994)
2.5×10^{-6}	Seawater, warm, dark	(Sinton et al., 1994)
7.6×10^{-5}	Seawater, sunlight	(Sinton et al., 1994)
1.1×10^{-4}	Seawater, sunlight	(Sinton et al., 1994)
4.7×10^{-4}	Seawater, sunlight	(Davies-Colley et al., 1994)
4.7×10^{-6}	Seawater, dark	(Sinton et al., 2002)
3.3×10^{-6}	River water, dark	(Sinton et al., 2002)
4.4×10^{-5}	Seawater, sunlight	(Sinton et al., 2002)
2.1×10^{-4}	Seawater, sunlight	(Sinton et al., 2002)
5.0×10^{-5}	River water, sunlight	(Sinton et al., 2002)
1×10^{-4}	River water, sunlight	(Sinton et al., 2002)
1.4×10^{-6}	Seawater, dark	(Sinton et al., 1999)
9.2×10^{-5}	Seawater, sunlight	(Sinton et al., 1999)
3.1×10^{-6}	Seawater, dark[2]	
7.8×10^{-6}	Seawater, dark[2]	

[1] Donna Ferguson, Orange County Health Care Agency, personal communication, February 2004.

[2] Unpublished data collected by Boehm et al. (2004).

3.2.4.1. Grazing experiments. To determine g, we follow the dilution method described by Landry and Hassett (1982) originally developed to estimate grazing on phytoplankton. This method is based on the assumptions that (1) growth or death of ENT is not influenced by the presence or absence of other ENT, (2) the probability of ENT being consumed is a direct function of grazer encounter with the bacteria and does not depend on the nutritional state of the prey, and (3) $C(t) = C_0 \exp(-k - g)t$, where C is the concentration of ENT as a function of time t, C_0 is the concentration of prey at $t = 0$, k is the ENT growth or inactivation rate and g is the rate of mortality due to ingestion by all size classes of grazers. Assumption 2 is equivalent to assuming that the grazers are not food-satiated, and their consumption increases linearly with prey density. Readers are referred to Landry and Hassett (1982) for a complete description of the theory.

Given these assumptions, g can be determined by comparing the decline in ENT over time in at least two experiments with different ratios of 0.22 μm filtered to unfiltered seawater. By combining different proportions of filtered and unfiltered seawater, one dilutes the effect of grazing by the same percent as unfiltered seawater is diluted by filtered seawater.

Forty liters of seawater were collected from the middle of the surf zones of both Santa Cruz (SC) and HB, California. Care was taken to avoid damage to organisms, including zooplankton, by filling collapsible containers slowly from the bottom.

Three liters of each water sample was vacuum filtered through a 0.22 μm pore size filter. Five hundred milliliter duplicate dilutions were set up with the following ratios of unfiltered to filtered seawater: 1:0, 3:1, 1:1, and 1:3. ENT were seeded into the 500 mL bottles so that the initial concentration was approximately 1000 cells/mL. The seed organisms were isolated from bird feces deposited on HB, and grown overnite in mE broth. An aliquot of log-phase organisms was washed three times with filtered seawater, and stored at 4 °C until used to seed bottle experiments. It should be noted that unfiltered seawater contained grazers of all sizes including bacterivorous protozoa and zooplankton; thus, g represents biologically mediated removal by multiple size classes.

Duplicate 10 mL samples were collected from each bottle at time 0 and analyzed for ENT. Bottles were incubated at 15 °C (similar to ambient coastal water temperatures) in the dark. After 24 h, duplicate 10 mL samples were collected. All samples were analyzed using EPA method 1600 in duplicate using undiluted, 10^{-1}, and 10^{-2} diluted samples. The 10^{-2} dilutions were used in all cases for quantifying the concentration of ENT present. The apparent rate of change of ENT concentrations ($1/t \ln(C(t)/C_0)$) was subsequently determined, following the methods outlined by Landry and Hassett (1982). Apparent growth or death rate for each dilution was plotted versus the fraction of unfiltered seawater in that experiment. The zooplantkon grazing rates g were determined using a linear-regression of these data. The negative slope of the line represents g.

To obtain a count and speciation of zooplankton greater than 75 μm in size, 22.5 L (HB) and 25 L (SC) of seawater were filtered through 75 μm mesh. Material retained on the mesh was subsequently washed with 10–30 mL 70% ethanol into centrifuge tubes, and stored at 4 °C for further analysis. Five hundred microliter aliquots of 75 μm concentrate were examined under 30 × magnification after staining with Bengal Rose to determine the types of zooplankton present in the surf zone waters. It should be noted that this method does not allow determination of the types or concentrations of grazers smaller than 75 μm, although they are certainly present and undoubtedly contribute to g.

4. Results and discussion

4.1. Length of shoreline adversely impacted by ENT

The first goal of our work is to predict the length of shoreline adversely impacted by a momentumless ENT point source at N and S beaches under wave conditions that create up- and downcoast littoral currents during a typical dry season. In order to estimate l_{eff}, we use l_{dil} from the literature (Boehm, 2003), and l_{die} and l_{graz} estimates described below.

4.1.1. Length scale due to grazing, l_{graz}

4.1.1.1. Grazing experiments. The raw data from the two grazing experiments are shown in Table 3. Results are summarized in Fig. 5, where the apparent rate of change in ENT is shown as a function of fraction of unfiltered water in HB and SC seawaters. The data points from duplicate bottle experiments are shown. There is some disagreement between the calculated apparent rate of change of ENT between replicate experiments. This could be due to imprecision in our enumeration technique or a non-uniform distribution of grazers in the unfiltered water. Disagreement between replicate grazing experiments using environmental waters is not unusual; Landry and Hassett (1982) report similar disagreement in their method paper. Despite the scatter in the data, the grazing rate (deemed from the slope of the lines fit to the data) estimated from both sets of experiments were quite similar, $g_{\text{SC}} = 0.59\,\text{d}^{-1}$ ($p<0.05$) and $g_{\text{HB}} = 0.52\,\text{d}^{-1}$ ($p<0.1$). The death/growth rate (y-intercept) varied in the experiments with SC and HB seawater probably because at the onset of the experiments ENT were experiencing different injury levels (Gauthier et al., 1992). This should not impact the reported grazing rates because, as mentioned in the Materials and Methods section, it is assumed that the nutritional/injury state of ENT does not influence the rate at which they are grazed. In our calculations of l_{graz}, we used the average of these two values $g = 0.56\,\text{d}^{-1}$ (or $6.5\times10^{-6}\,\text{s}^{-1}$). This value is within the range of grazing mortality rates reported by Menon et al. (2003) for *Streptococcus faecium* in the North Sea, despite the fact that the authors used a different method for quantifying grazing.

Table 3
The results of grazing experiments

Fraction unfiltered seawater	C_0	C_1	Apparent rate of change (d^{-1})
Huntington Beach seawater			
0.25	780	600	−0.26
0.25	800	480	−0.51
0.5	650	650	0.0
0.5	760	470	−0.48
0.75	720	450	−0.47
0.75	900	420	−0.76
1	860	460	−0.63
1	800	370	−0.77
Santa Cruz seawater			
0.25	270	375	0.33
0.25	425	480	0.12
0.5	375	360	−0.04
0.5	460	375	−0.20
0.75	410	410	0.00
0.75	295	325	0.10
1	475	375	−0.24
1	420	280	−0.41

Reported concentrations are averages of two plate counts. C_0 and C_1 are concentrations of ENT in units of colony forming units (CFU) per mL at the onset of the experiments and after 1 d had elapsed, respectively.

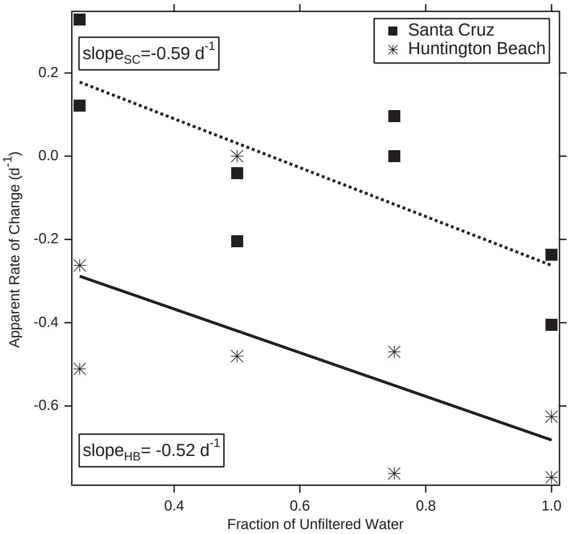

Fig. 5. Results from the grazing experiment modified from Landry and Hassett (1982). The apparent rate of change in ENT is shown as a function of fraction of unfiltered seawater for two sets of experiments conducted with waters from different locations. Linear curve-fits were generated using a least-squares algorithm. Corresponding slopes are shown.

Microscopic analyses of the greater than 75 µm fraction of both HB and SC surf zone waters revealed the presence of many different types of zooplankton. The classes and concentrations were similar in both samples. The following organisms were observed: copepods (approximately 200 copepods per L), ciliates, bivalves, Foraminifera, Hydrozoa, and gastropods. These organisms are typical of nearshore coastal waters (Todd et al., 1996). We did not attempt to identify or enumerate other bacterivorous organisms present in the unfiltered fraction of seawater, although they certainly contribute to our measured g.

4.1.1.2. l_{graz}. The frequency distribution of alongshore currents typical during JJA was used with the average grazing rate estimated from the grazing experiments to calculate l_{graz}. The resulting distribution of length scales is shown in Fig. 6 Panel A for N and S beaches when alongshore currents are oriented in an up- or downcoast direction. The smallest l_{graz} are between 1000 and

4000 m and observed at N beaches during upcoast littoral drift (52% of total estimates). These occur when the alongshore currents are small like those that would result from a south-southwest swell (Table 1). The remaining l_{graz} predicted for upcoast littoral drift conditions are between 32,000 and 125,000 m. At N beaches under downcoast drift conditions, 100% of the estimates are between 32,000 and 125,000 m. At S beaches during upcoast flow, 90% of l_{graz} estimates are between 32,000 and 63,000 m. At S beaches when currents are directed downcoast, l_{graz} ranges from 63,000 to 250,000 m. The implications of these length scales on the relative contribution of grazing to the alongshore attenuation of ENT at the field site will be discussed in following sections. It is important to note that the majority of the predicted length scales are approximately an order of magnitude greater than l_{dil} in Fig. 4 Panel B, with the exception of relatively small l_{graz} estimated at N beaches during upcoast littoral drift.

4.1.2. *Length scale due to inactivation, l_{die}*

The inactivation rates taken from the literature (Table 2) were used along with the q_{l} distributions typical for JJA (Fig. 4 Panel A) to determine l_{die}. The results are shown in Fig. 6 Panel B. At N beaches, when alongshore currents are in the upcoast direction, 60% of the l_{die} estimates range from 4000 to 8000 m and nearly 30% of the estimates are between 8000 and 16,000 m. When downcoast currents are generated by the prevailing waves, 38% of l_{die} estimates at N beaches range from 4000 to 16,000 m and 52% from 126,000 to 250,000 m. At S beaches, l_{die} is distributed similarly during upcoast and downcoast alongshore flow, with the slightly smaller length scales during upcoast flow. When currents are in the upcoast direction, l_{die} ranges from 1000 to 16,000 m (43% of estimates) and 63,000 to 250,000 m (57% of estimates). When currents are oriented in the downcoast direction, l_{die} ranges from 4000 to 32,000 m (43% of estimates) and 63,000 to 500,000 m (57% of estimates). As with l_{graz}, the l_{die} estimates are large relative to the l_{dil} estimates reported for the field site. Compared to l_{graz}, the length scale for inactivation typically covers a larger range of values.

4.1.3. *Calculation of l_{eff}*

The length scale over which ENT from a point source decays *e*-fold from its value at the source (l_{eff}) was estimated from l_{dil}, l_{die}, and l_{graz} using Eq. (4b) for N and S beaches during up- and downcoast littoral drift. The resulting distributions are shown in Fig. 6 Panel C.

At N beaches during upcoast flow, 50% of l_{eff} estimates are quite small, on the order of 10 m. This small length scale occurs when the processes we are considering are rapid. The remainder of the estimates are primarily distributed between 1000 and 3000 m (40%), with some estimates (4%) between 7000 and

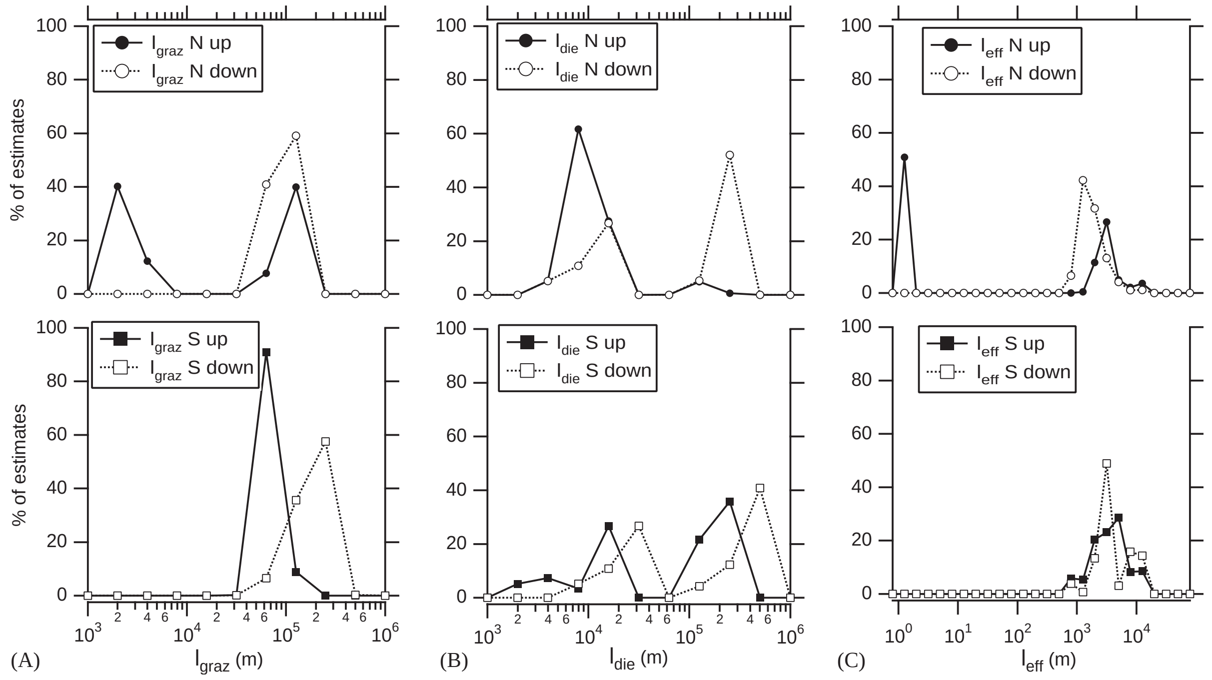

Fig. 6. Frequency distributions of l_{graz} (panel A), l_{die} (panel B), and l_{eff} (panel C) calculated for ENT up- (filled symbols, solid line) and downcoast (open symbols, dotted line) of N (circles) and S (squares) beaches. The frequency with which values are observed for each bin is denoted by a marker placed at the highest end of each bin.

13,000 m. When alongshore currents are oriented downcoast, l_{eff} is primarily distributed between 800 and 3000 m (94% of estimates).

At S beaches, during upcoast flow, l_{eff} is predicted to fall between 1000 and 13,000 m with 70% of the estimates between 1000 and 5000 m. When currents are oriented downcoast, 50% of l_{eff} range from 2000 to 3000 m and 30% range from 5000 to 13,000 m.

There are two important assumptions to revisit while interpreting these values. First, we assumed that ENT removal processes other than grazing and inactivation (i.e., sedimentation and viral lysis) are not important. If other processes actually were important, then l_{eff} would be reduced, as Eq. (4b) would contain one or more additional terms in the denominator (e.g., l_x^{-1} where x is the removal mechanism). The degree to which l_{eff} would be reduced depends on the strength of the removal mechanism. Second, we assumed that l_{dil} from Boehm (2003) were reasonable estimates for the field site. We mentioned earlier that they could be viewed as lower bounds for real l_{dil}. According to Eq. (4b), if l_{dil} were actually higher, then l_{eff} would also be increased.

4.2. Does grazing, inactivation, or dilution dominate ENT attenuation within the surf zone?

To understand which processes (dilution, inactivation, and grazing) are most important in controlling l_{eff}, we examined the non-dimensional parameters Γ and Φ predicted from the model (Fig. 7). Γ, as defined in Eq. (5a), can range from 0 when the length scale over which ENT are attenuated due to inactivation is large relative to actual length scale of attenuation (indicating inactivation is not important) to 1, when l_{die} and l_{eff} are comparable in magnitude indicating inactivation contributes to the attenuation of ENT significantly. In Fig. 7 Panel A, Γ for beaches in our study area are shown for the different littoral drift conditions. At N beaches during upcoast flow, approximately 40% of the estimates for Γ are on the order of 10^{-3} and 50% are between 0.1 and 0.4—the largest estimate for upcoast Γ. When currents are generated in the downcoast direction, the smallest Γ estimate is 0.01 and the largest is 0.4. The majority of the downcoast Γ estimates (70%) are between 0.01 and 0.1, with the remainder (30%) between 0.1 and 0.4. At S beaches, during upcoast drift, Γ ranges from 0.03 to 0.6 (the highest Γ value estimated under any condition). There are two peaks in the distribution, one centered at 0.04 and another at 0.4. The distributions about these peaks represent 58% and 42% of the estimates, respectively. When currents are oriented in the downcoast direction, Γ ranges from 0.01 to 0.4. The distribution is bimodal with peaks at 0.02 and 0.15, the distributions about the peaks represent 58% and 42% of the estimates, respectively (the same proportions as for the upcoast littoral drift conditions). Overall, these

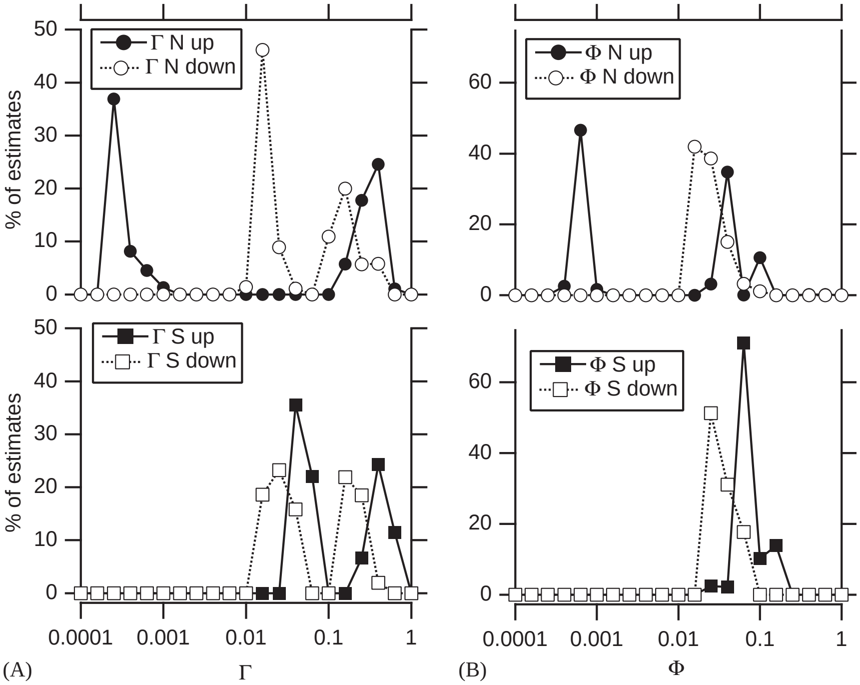

Fig. 7. Frequency distributions of Γ (panel A) and Φ (panel B) calculated for ENT up- (filled symbols, solid line) and downcoast (open symbols, dotted line) of N (circles) and S (squares) beaches. The frequency with which values are observed for each bin is denoted by a marker placed at the highest end of each bin.

results suggest that inactivation influences the effective length scale of ENT pollution at these beaches under some conditions when $\Gamma > 0.1$, while under other conditions, Γ is sufficiently small that inactivation does not influence ENT relative to dilution and grazing.

Φ describes the importance of grazing in attenuating levels of ENT away from a point source and is defined in Eq. (5b). If $\Phi = 1$, grazing alone can account for the decline in ENT levels away from a point source. If $\Phi = 0$, then l_{eff} is sufficiently small compared to the length scale for grazing that grazing can be deemed unimportant. The estimates of Φ obtained for the field site are shown in Fig. 7 Panel B. In all but a few cases, Φ is less than 0.1, indicating that l_{graz} is large relative to l_{eff}, and thus, grazing plays a minor role relative to other factors as a sink for ENT in the surf zone. The only instances where $\Phi > 0.1$ are as follows. During upcoast littoral transport at N and S beaches, 0.4% and 15% of the Φ estimates are greater than 0.1. The results for Φ suggest that grazing is important only under special circumstances when alongshore currents are fast, and inactivation rates are slow, as might be the case when large waves impinge upon the coast at an oblique angle and in dark conditions (Table 2).

Fig. 8 permits visualization of how the processes of grazing, inactivation, and dilution act in synergy to control ENT levels at the field site (a practical application of Fig. 2). In this figure, 10,000 pairs of Γ and Φ estimated from our simulations are plotted versus one another. The fact that most of the data points fall close to the line $\Phi = 0$ indicates that dilution and inactivation are more important in controlling ENT levels than grazing. There are a few instances where all three parameters are important and this occurs at N beaches when currents are directed upcoast (black circles in the middle of the triangle). Because so many of the data points fall close to the point (0,0), dilution consistently plays a major role in controlling ENT levels in the surf zone of the study area.

In revisiting our assumptions as we did above for l_{eff}, if there are important removal mechanisms we have not considered, both Γ and Φ would be reduced, shifting points closer to the origin of Fig. 8. Such a shift further de-emphasizes the importance of inactivation and grazing, and suggests dilution is even more important. It should be noted, however, that an additional interpretation of points near the origin of Fig. 8 is that a neglected removal mechanism is important rather than dilution. If l_{dil} in Fig. 4 Panel B are underestimates and true l_{dil} were higher, then both Γ and Φ would increase, implying that inactivation and grazing are actually more important than suggested by Fig. 8.

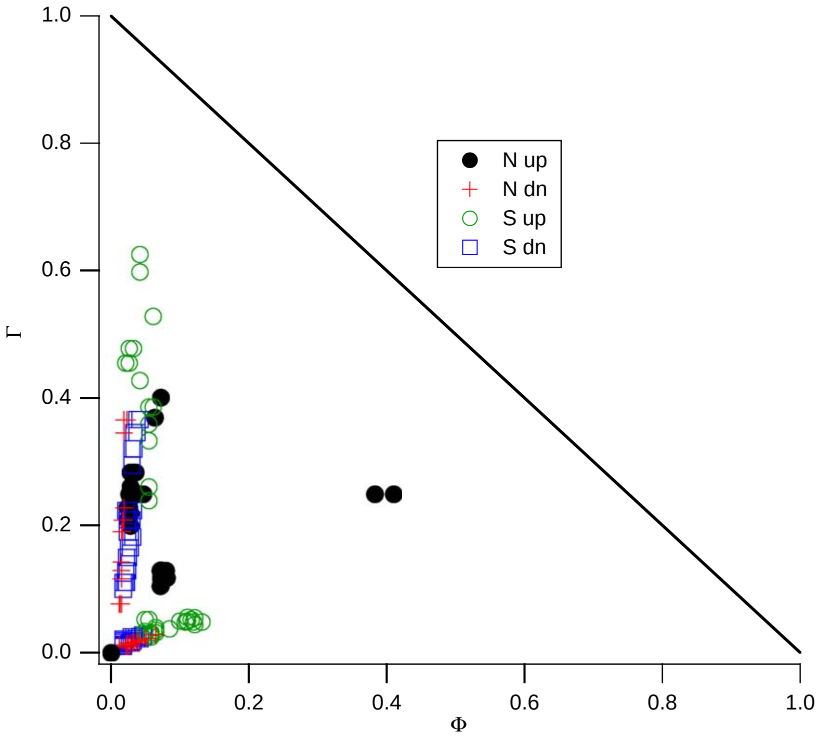

Fig. 8. Γ as a function of Φ for 10,000 Monte Carlo simulations. See Fig. 2 for theoretical explanation of plot. Different symbols correspond to predictions for variables at N or S beaches during up- or downcoast littoral drift conditions (upper right corner).

5. Implications

We present estimates of grazing rates for ENT in a marine surf zone on the order of $10^{-6}\,\mathrm{s}^{-1}$. This is the same order of magnitude estimated by Landry and Hassett (1982) for grazing mortality of phytoplankton in coastal waters off Washington, USA, during the fall. The estimates are also within the range reported by Menon et al. (2003) for grazing of *S. faecium* in the North Sea, though these researchers used a different method for estimating grazing rates. g is within the same order of magnitude as several ENT inactivation rates published in the literature (Table 2). Thus, in some cases losses due to consumption by grazers may be comparable to losses due to inactivation, especially in areas where dilution is minimal (e.g., an enclosed tide-dominated bay) and inactivation rates are slow (e.g., during dark conditions). Because grazing mortality is dependent on the number of bacterivorous organisms present in the water, it is expected to vary seasonally as the number and types of bacterioplankton in the water column vary. The estimates for g presented in this paper should be viewed as first-order estimates given the dynamic nature of microbial food webs.

According to our model that considers dilution, inactivation, and grazing, the length of shoreline impacted by a point source of ENT falls primarily between 1000 and 5000 m. Some estimates are beyond this range; for example, during upcoast littoral drift at N beaches, 50% of the time, the length scale is on the order of 10 m.

Values of the non-dimensional parameters Γ and Φ indicate that dilution is the primary process controlling the alongshore attenuation of ENT. Inactivation is of secondary importance, and at this field site influences ENT fate when alongshore currents are oriented in the upcoast direction at both N and S beaches. This could occur with the coincidence of fast littoral currents caused by larger than average waves from the south and relatively high inactivation rates. Overall, grazing plays a tertiary role, but in some instances, especially when dilution and inactivation rates are relatively low, can serve as an important sink for ENT. This case is most often observed during upcoast flow at both beaches.

The importance of dilution in controlling ENT levels away from a point source suggests that strategic placement and timed releases of ENT-rich effluent during periods of high dilution would result in a smaller length of shoreline impacted by elevated ENT. Placement of point sources should be at beaches with steep slopes (small x_b) or beaches subjected to large waves whose angle of attack produces small q_l. Releases could be timed to coincide with large waves whose angle of attack produces small q_l (such as waves from the south-southwest at N beaches at this field site).

The results presented here are limited by our understanding of the transport and extra-enteric ecology of ENT in the marine surf zone environment. Future work should address the mechanisms of inactivation, physically mediated removal of ENT from the water column, and viral lysis of ENT by natural populations of bacteriophage. A more detailed understanding of transport in the surf zone is also needed.

Acknowledgements

Deyi Hou compiled the inactivation data. Alyson Santoro assisted in the grazing experiments. Oliver Fringer provided assistance on a portion of the manuscript. We acknowledge two anonymous reviewers and the editor for constructive comments that significantly improved the manuscript. The Powell Foundation, Clare Luce Boothe professorship, UPS Foundation, and a NOAA Oceans and Human Health grant are acknowledged for support. D. P. K. was supported by Stanford Institute for the Environment.

References

Barcina, I.P., LeBaron, P., Vives-Rego, J., 1997. Minireview. Survival of allochthonous bacteria in aquatic systems: a biological approach. FEMS Microbiol. Ecol. 23 (1), 1–9.

Boehm, A.B., 2003. Model of microbial transport and inactivation in the surf zone and application to field measurements of total coliform in northern orange county, California. Environ. Sci. Technol. 37 (24), 5511–5517.

Boehm, A.B., Grant, S.B., Kim, J.H., McGee, C.D., Mowbray, S., Clark, C.D., Foley, D., Wellmann, D., 2002. Decadal and shorter period variability of surf zone water quality at Huntington Beach CA. Environ. Sci. Technol. 36 (18), 3885–3892.

Cheng, N.S., Law, A.W., Findikakis, A.N., 2000. Oil transport in surf zone. J. Hydraulic Eng. 126 (11), 803–809.

Davies-Colley, R.J., Bell, R.G., Donnison, A.M., 1994. Sunlight inactivation of enterococci and fecal coliforms in sewage effluent diluted in seawater. Appl. Environ. Microbiol. 60 (6), 2049–2058.

Desmarais, T.R., Solo-Gabriele, H.M., Palmer, C., 2002. Influence of soil on fecal indicator organisms in a tidally influenced subtropical environment. Appl. Environ. Microbiol. 68 (3), 165–1172.

Gauthier, M.J., Flatau, G.N., Clement, R.L., Munro, P.M., 1992. Sensitivity to *Escherichia coli* to seawater closely depends on their growth stage. J. Appl. Bacteriol. 73 (3), 257–262.

Grant, S.B., Webb, C., Sanders, B.F., Jones, B., Boehm, A., Kim, J.H., Redman, J., Chu, A., Mrse, R., Gardiner, N., Brown, A., 2000. Huntington beach water quality investigation phase II: an analysis of ocean, surf zone, watershed, sediment, and groundwater data collected from June 1998 to September 2000. Technical Report, City of Huntington Beach.

Grant, S.B., Sanders, B.F., Boehm, A.B., Redman, J.A., Kim, J.H., Mrse, R.D., Chu, A.K., Gouldin, M., McGee, C.D., Gardiner, N.A., Jones, B.H., Svejkovsky, J., Leipzig, G.V., Brown, A., 2001. Generation of enterococci bacteria in a coastal salt water marsh and its impact on surf zone water quality. Environ. Sci. Technol. 35 (12), 2407–2416.

Hanes, N.B., Fragala, R., 1967. Effect of seawater concentration on survival of indicator bacteria. J. Water Pollution Control Federation 39 (1), 97–104.

Hartke, A., Lemarinier, S., Pichereau, V., Auffray, Y., 2002. Survival of *Enterococcus faecalis* in seawater microcosms is limited in the presence of bacterivorous zooflagellates. Current Microbiol. 44 (5), 329–335.

Inman, D.L., Brush, B.M., 1973. The coastal challenge. Science 181 (4094), 20–32.

Inman, D.L., Tait, R.J., Nordstrom, C.E., 1971. Mixing in the surf zone. J. Geophys. Res. 76 (15), 3493.

Landry, M.R., Hassett, R.P., 1982. Estimating the grazing impact of marine micro-zooplankton. Mar. Biol. 67 (3), 283–288.

Longuet-Higgens, M.S., 1970a. Longshore currents generated by obliquely incident waves. J. Geophys. Res. 75 (33), 6790–6801.

Longuet-Higgens, M.S., 1970b. Longshore currents generated by obliquely incident waves. I. J. Geophys. Res. 75 (33), 6778–6790.

McCambridge, J., McMeekin, T.A., 1981. Effect of solar radiation and predacious microorganisms on survival of fecal and other bacteria. Appl. Environ. Microbiol. 41 (5), 1083–1087.

Menon, P., Billen, G., Servais, P., 2003. Mortality rates of autochthonous and fecal bacteria in natural aquatic ecosystems. Water Res. 37 (17), 4151–4158.

Noble, R.T., Lee, I.M., Schiff, K.C., 2004. Inactivation of indicator microorganisms from various sources of faecal contamination in seawater and freshwater. J. Appl. Microbiol. 96, 464–472.

Nystrom, T., 2004. Stationary-phase physiology. Ann. Rev. Microbiol. 58, 161–181.

Rabinovici, S.J.M., Bernknopf, R.L., Wein, A.M., Coursey, D.L., Whitman, R.L., 2004. Economic and health risk trade-offs of swim closures at a Lake Michigan beach. Environ. Sci. Technol. 38 (10), 2737–2745.

Rijn, L.C.V., 1998. Principle of Coastal Morphology. Aqua Publications, Amsterdam, The Netherlands.

Sinton, L.W., Davies-Colley, R.J., Bell, R.G., 1994. Inactivation of enterococci and fecal coliforms from sewage and meatworks effluents in seawater chambers. Appl. Environ. Microbiol. 60 (6), 2040–2048.

Sinton, L.W., Finlay, R.K., Lynch, P.S., 1999. Sunlight inactivation of fecal bacteriophages and bacteria in sewage-polluted seawater. Appl. Environ. Microbiol. 65 (8), 3605–3613.

Sinton, L.W., Hall, C.H., Lynch, P.A., Davies-Colley, R.J., 2002. Sunlight inactivation of fecal indicator bacteria and bacteriophages from waste stabilization pond effluent in fresh and saline waters. Appl. Environ. Microbiol. 68 (3), 1122–1131.

Todd, C.D., Laverack, M.S., Boxshall, G.A., 1996. Coastal Marine Zooplanton: A Practical Manual for Students. Cambridge University Press, New York, NY.

Wade, T.J., Pai, N., Eisenberg, J.N.S., Colford, J.M., 2003. Do US environmental protection agency water quality guidelines for recreational waters prevent gastrointestinal illness? A systematic review and meta-analysis. Environ. Health Perspectives 111 (8), 1102–1109.