Between tide and wave marks: a unifying model of physical zonation on littoral shores

The effects of tides on littoral marine habitats are so ubiquitous that shorelines are commonly described as 'intertidal', whereas waves are considered a secondary factor that simply modifies the intertidal habitat. However mean significant wave height exceeds tidal range at many locations worldwide. Here we construct a simple sinusoidal model of coastal water level based on both tidal range and wave height. From the patterns of emergence and submergence predicted by the model, we derive four vertical shoreline benchmarks which bracket up to three novel, spatially distinct, and physically defined zones. The (1) emergent tidal zone is characterized by tidally driven emergence in air; the (2) wave zone is characterized by constant (not periodic) wave wash; and the (3) submergent tidal zone is characterized by tidally driven submergence. The decoupling of tidally driven emergence and submergence made possible by wave action is a critical prediction of the model. On wave-dominated shores (wave height >> tidal range), all three zones are predicted to exist separately, but on tide-dominated shores (tidal range >> wave height) the wave zone is absent and the emergent and submergent tidal zones overlap substantially, forming the traditional "intertidal zone". We conclude by incorporating time and space in the model to illustrate variability in the physical conditions and zonation on littoral shores. The wave:tide physical zonation model is a unifying framework that can facilitate our understanding of physical conditions on littoral shores whether tropical or temperate, marine or lentic.

1   Christopher E. Bird[1,2], Erik C. Franklin[2], Celia M. Smith[3] and Robert J. Toonen[2]

4   [1]Texas A&M University - Corpus Christi, Department of Life Sciences, 6300 Ocean Drive,

5   Corpus Christi, TX 78412-5802

6   [2]Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, HI 96744

7   [3]Department of Botany, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822

INTRODUCTION

9   Littoral habitats, those lying between the low-tide line and the upper limit of aquatic

10   species on the shore, are among the most studied and well-known aquatic habitats. Much

11   attention has been devoted to the study of organisms on rocky shores - in particular their vertical

12   zonation, the upper and lower limits of species, and distribution along gradients of wave

13   exposure. Hypotheses addressing the causes of biotic zonation and community structure have

14   evolved from strictly physical to an inseparable combination of physical and biological factors,

15   including physiological tolerance and species interactions . Throughout the progression of

16   intertidal zonation research, the most widely accepted paradigm has remained that the predictable

17   pattern of tidal rise and fall is the "primary" mechanism affecting shoreline water levels and the

18   littoral habitat .

19   Stephenson and Stephenson proposed their "universal features of zonation between tide-

20   marks on rocky coasts" after conducting surveys of vertical biotic zonation on littoral shores

21   world-wide. While the model of Stephenson and Stephenson (1972) focuses on biotic zonation,

22   it is essentially a physical model based on the concept that there is a classic intertidal zone

23   (midlittoral zone = balanoid zone), a transition zone between the intertidal zone and the terrestrial

24   biosphere (supralittoral fringe = *Littorina* zone), and a transition zone between the intertidal zone

25   and subtidal biosphere (infralittoral fringe = laminarian zone). One of the benefits of focusing on

26   the biota, rather than elevation, was that these zones were not found predictably at the same

27   height above sea level either within or among geographic regions. "Secondary modifying

28   factors" of littoral climate, such as waves, were thought to enlarge and/or elevate the basic zones,

29   but not change their primary properties . More recent research continues to demonstrate that

30   biotic zones and species distribution limits do not consistently occur at the same shore levels,

31   even within shores .

32   A fundamental advance in the understanding of biotic zonation on rocky shores was the

33   demonstration that species interactions also affected zonation patterns, where biotic factors

34   generally determine the lower limit of distribution and physical factors affect the upper limit of

35   distribution . A number of exceptions to this generalization have been demonstrated , many of

36   which highlight the effect of biotic interactions on the realized distribution of a species. These

37   examples demonstrate that biotic factors can also regulate the upper limits of a species'

38   distribution, but focus on the proximate factors affecting realized species distributions.

39   Ultimately, the inseparable interaction between physical and biotic factors define the realized

40   limits of species , and models of physical clines can contribute valuable information to elucidate

41   biotic processes . Indeed,

42   "rocky shores are the 'stage' upon which ecological 'dramas' are played out, and

43   physical conditions both provide the 'ambiance' and help direct the 'plays' ."

44   Consequently, a more predictive model of physical habitat zonation on littoral shores would be

45   very valuable.

46   Patterns of changing community structure and composition along wave exposure

47   gradients have not typically been viewed as an issue of zonation. Instead, shifts in community

48   structure along wave exposure gradients have traditionally been associated with the effects of

49   hydrodynamic force (physical stress and disturbance) on biotic interactions . This is an

50   oversimplification, however, because with increasing wave exposure factors other than

51   hydrodynamic force are at play on shores where wave heights approach or exceed the tidal range.

52   More recent studies demonstrate that waves also affect patterns of community composition along

53   wave exposure gradients by creating habitat with associated physiological stress and disturbance

54   that does not exist on more wave protected shores . In particular, GIS-based models of wave

55   exposure and quantitative metrics of effective fetch can explain a considerable proportion of

56   variance in species abundances among sites at some locations . Even so, the manner and

57 mechanism by which waves interact with tides to create littoral habitat and the subsequent effects

58 on biological processes have yet to be fully explored.

59 Here we investigate the roles of tides and waves in driving the characteristics of the

60 physical habitat by deriving a sinusoidal model of coastal water level. We begin with a model of

61 coastal water level based solely on tidal range and wave height. We use the model to derive

62 relevant physically-defined shoreline benchmarks and partition the littoral zone into novel

63 habitats. In so doing, we develop a system for the generic physical quantification and

64 categorization of any shoreline across a range of spatial and temporal scales.

65

66 **MATERIALS AND METHODS**

67 **Model of coastal water level**

68 We construct our simple model of coastal water level using both tidal and wave signals.

69 First, we model the coastal water level (W) over time by summing sinusoidal models of water

70 level due to tidal (W_T) and wave action (W_W) as follows:

71 $$W_T = A_T + A_T \sin\left(\left|\frac{2\pi T}{P_T}\right|\right) \quad (1) \text{ (Fig. 1a)}$$

72 $$W_W = A_W \sin\left(\left|\frac{2\pi T}{P_W \cdot 3600}\right|\right) \quad (2) \text{ (Fig. 1b)}$$

73 $$W = W_T + W_W \quad (3) \text{ (Fig. 1c)}$$

74 where A_T is the tidal amplitude in meters, T is the time in number of hours, P_T is the tidal period

75 (P_T=12.2 h), A_W is the wave amplitude, and P_W is the wave period (P_W=10 s, note that the wave

76 period has been increased in the figures for aesthetic reasons). The goal of this model is to

77 grossly estimate the patterns of emersion and submersion experienced by shoreline organisms

78 and demonstrate the conceptual consequences of taking wave height into account. Many

79 additional factors interact with wave height to determine the extent of wave run-up and splash

80 and will affect patterns of emersion and submersion, especially among regions with semi-diurnal,

81 diurnal and semi-mixed tidal regimes, but incorporating that complexity is beyond the scope of

82 this effort and does not change our conclusions or the implications of the concepts developed

83 herein.

84

85   **Wave height and tidal range data**

86   Global maps of tidal range and satellite data on significant wave height which will be

87 exceeded 50% of the time were used to generate Fig. 3a. For Fig. 3b, significant wave heights

88 from the KNMI/ERA-40 Wave Atlas and tidal range from the TOPEX/POSEIDON 6.2

89 (TPXO6.2) data sets were used. The KNMI/ERA-40 Wave Atlas data were derived from the

90 reanalysis of oceanographic and atmospheric data with the European Centre of Medium-Range

91 Weather Forecast's (ECMWF) Integrated Forecasting System coupled to the third generation

92 wave forecast WAM model . The diurnal tidal range was computed from the average maximum

93 daily range for each day (MHHW – MLLW) using 10 available tidal constituents from TPXO6.2 .

94 Wave height to tidal range ratios were calculated and mapped for a 2º x 2º global grid (Fig. 3b)

95 with Matlab 7.5 (MathWorks, Natick, Massachusetts) and ArcGIS 9.2 (ESRI, Redlands,

96 California). Tide and wave heights can vary on small spatial scales; therefore, we expect there to

97 be heterogeneity in the ratio of wave height to tidal range at smaller spatial scales than can be

98 represented in a global map. For example, although the Hawaiian Archipelago is classified as

99 wave-dominated, shorelines behind shallow reef crests which cause waves to break will be

100 mostly tide-dominated. Microsoft Excel 2003 and Visual Basic for Applications (Microsoft

101 Corp., Seattle, Washington), was the software modeling environment used to generate all

102 statistics and figures unless otherwise noted above.

103   On a finer scale, we selected three specific sites that, on average, exhibit wave-dominated

104 (Mokapu, Hawai'i), co-dominated (Humboldt, California), and tide-dominated conditions

105 (Portland, Maine) to illustrate how their differences affect model predictions (locations marked

106 with stars, Fig. 3a). Real, not predicted, historical data on significant wave height and tidal range

107 (MHHW - MLLW) were extracted from the National Oceanographic and Atmospheric

108 Administration (NOAA) National Data Buoy Center (www.ndbc.noaa.gov) and NOAA National

109 Ocean Service oceanographic products (www.tidesandcurrents.noaa.gov), respectively. The

110 wave buoys were located at Mokapu, Hawai'i (station 51202, 2000-2005), Humboldt South Spit,

111 California (station 46212, 2004-2005), and Portland, Maine (station 44007, 1982-2001). The tide

112 stations were located at Moku O Lo'e, Hawai'i (station 1612480, National Ocean Service

113 Waimanalo tide correction applied), North Spit, California (station 9418767), and Portland,

114 Maine (station 8418150).

115

116

117 **RESULTS**

118 **Derivation of shoreline benchmarks and zones**

119 We begin by exploring the sinusoidal water level model which incorporates both tidal

120 range and wave height for a single tidal cycle (Eq. 3, Fig. 1c). Four specific benchmarks

121 associated with submersion and emersion can be derived from the basic model, Benchmarks 1-4

122 (Fig. 2). Benchmark one (B_1) is the height of the upper reach of the wave crests at high tide and

123 is defined as:

$$B_1 = A_H + 2A_t + W_{Tlow} \quad (4)$$

125 where W_{Tlow} is the water level at low tide relative to MLLW (see Methods for definitions of other

126 variables). Benchmark two (B_2) is the height of the upper reach of wave crests at low tide and is

127 defined as:

$$B_2 = A_H + W_{Tlow} \quad (5)$$

129   Benchmark three (B_3) is the height of the lower reach of the wave troughs at high tide and is

130   defined as:

131                                     $B_3 = 2A_T + W_{Tw} - A_T$ (6)

132   Benchmark four (B_4) is the height of the lower reach of wave troughs at low tide and is defined

133   as:

134                                     $B_4 = W_{Tw} - A_T$ (7)

135   In the model, benchmarks one (blue) and four (black) mark the boundaries above which

136   there is constant emersion and below which there is constant submersion, respectively (Fig. 2).

137   Benchmark two (green) marks the lowest position on the shore that experiences tidally induced

138   periods of emersion, and benchmark three (pink) marks the highest position on the shore that

139   experiences tidally induced submersion. Benchmarks 1-4 can be used to define discrete shoreline

140   zones. Benchmarks one (blue) and two (green) bracket a zone of tidally induced emersion (Figs.

141   2 h,i), that we term the emergent tidal zone (vertical bars Figs. 2e,f). Similarly, benchmarks three

142   (pink) and four (black) demarcate a zone of tidally induced submersion (Figs. 2 h,i), that we label

143   the submergent tidal zone (horizontal bars, Figs. 2e,f). Where these zones overlap (Fig. 2d,g), a

144   zone of tidally induced emersion and submersion occurs – the traditional notion of an "intertidal

145   zone" and roughly equivalent to the mid littoral zone of Stephenson and Stephenson . A third

146   zone, bracketed by benchmarks two (green) and three (pink), is sandwiched between the

147   emergent and submergent tidal zones when wave height is greater than tidal range and is termed

148   the wave zone because it is washed by waves at both high and low tide (Fig. 2f,i).

149

150   **Derivation of physical categories for shorelines**

151   Our model of shoreline water level predicts three primary categories for intertidal shores:

152   tide-dominated, wave-dominated, and co-dominated (Fig. 2). When a shore is tide-dominated,

153 tidal range is much greater than wave height and there is substantial overlap of the emergent and

154 submergent tidal zones (Figs. 2a,d,g). When a shore is wave-dominated, wave height is much

155 greater than tidal range and all three zones (emergent, wave, and submergent) exist independently

156 (Figs. 2c,f,i). The third category, co-domination, occurs when wave height = tidal range, and is

157 characterized by non-overlapping emergent and submergent intertidal zones, but no wave zone

158 (Figs. 2b,e,h).

159

160   **Global categorization of shorelines**

161   A strength of our intertidal zonation model is that it can be applied across a variety of

162 spatial and time scales. At a global spatial scale over a number of years, averaged data for wave

163 height and tidal range can be used to classify shores as tide-, wave-, or co-dominated (Fig. 3).

164 The most striking feature of Fig. 3 is that the majority of offshore oceanic islands are predicted to

165 be wave-dominated (Fig. 3b) and the majority of continental shores are predicted to be tide-

166 dominated on average (Fig. 3a). There are also numerous areas of co-domination and wave-

167 domination on continental shores. Wave-dominated shores are most prevalent in the Southern

168 Ocean where winds blow around the globe with few land barriers and in freshwater lakes which

169 have negligible tidal action. It should be noted that tidal range and wave heights can vary on

170 small spatial scales; therefore, we expect there to be heterogeneity in the ratio of wave height to

171 tidal range at smaller scales than can be represented in an averaged global map (see the section

172 below). This is not a failure of the model, rather it is an issue with the scale of the data loading

173 the model. For example, although the Hawaiian Archipelago is classified as wave-dominated,

174 shorelines behind shallow reef crests which cause waves to break will be mostly tide-dominated.

175 If wave height data were collected on a fine scale to decipher fore reef from back reef, this

176 pattern would be captured. Additionally, there is temporal variation in tidal range and wave

177 heights which will cause temporal variation in the positions of Benchmarks 1-4, and could lead to

178 temporal variation in the classification of points on the shore as tide-, co-, or wave dominated.

179

180 **Temporal variation in zonation**

181 It is important to recognize that there is a continuum from tide-, to co-, to wave-

182 domination with no hard and fast boundaries, and the positions of Benchmarks 1-4 move as tidal

183 range and wave height varies. Although the long term averages presented in Figs. 3 and 4a-f are

184 informative, tidal range and wave heights are highly variable in time. Consequently, it is

185 important to be able to evaluate the variation in the position of Benchmarks 1-4 and the

186 associated physical littoral zones through time. We applied Equations 4-7, for predicting the

187 shore level of Benchmarks 1-4, to hourly wave height and tide measurements taken at Portland,

188 Maine; Humboldt, California; and Mokapu, Hawaii from June 2005 – June 2006 to evaluate the

189 variance in the predicted positions of the shoreline benchmarks on a fine temporal scale for one

190 year (Figs. 4g-i). The low tide line (W_{Tlow}) and tidal amplitude (A_T) for Equations 4-7 were

191 defined as the low tide level and the tidal amplitude during each semidiurnal tidal period,

192 maximizing variation induced by tides.

193 As expected, there was considerable fine scale variation in the model-predicted positions

194 of the benchmarks at all three sites, which varied by up to 3.8 m, 4.4 m, and 2.0 m at Portland,

195 Humboldt, and Mokapu, respectively (Figs. 4g-i). Portland is classified as tide-dominated (ratio

196 of wave height to tidal range < 0.5) for 82% of the year-long period (Fig. 4j, notice that B_2 is

197 consistently lower on the shore than B_3 indicating the overlap of the emergent intertidal and

198 submergent tidal). Mokapu is classified as wave-dominated (ratio of wave height to tidal range >

199 1.5) for 99% of the year-long period (Fig. 4l, notice that B_2 is consistently higher on the shore

200 than B_3).

201   Humboldt is an interesting case because it is predicted to be co-dominated for 48% and

202   wave-dominated for 48% of the year-long period on a fine temporal scale (Fig. 4k), but was

203   classified as co-dominated based on the yearly averaged diurnal tidal range and yearly mean

204   significant wave height (Fig. 4b). While there were portions of the winter where the significant

205   wave heights were consistently at least 1.5 times greater than the diurnal tidal range due to large

206   waves, most wave-dominated conditions were caused by large differences in the daily

207   semidiurnal tidal ranges - the smaller tidal range being wave-dominated and the greater tidal

208   range being co-dominated (causing the benchmark lines to appear thick in Fig. 4h). Ultimately,

209   Humboldt tends to be co-dominated by waves and tides on a diurnal scale in the summer and can

210   be wave-dominated in the winter, but also tends to alternate between co-domination and wave-

211   domination on a fine semidiurnal temporal scale. Overall, our model of coastal water level can

212   be used to effectively illustrate how patterns of wave and tide induced immersion vary at the

213   scale of a single tidal period and hundreds of tidal periods, facilitating the physical description of

214   sites in a concise and informative manner.

215

216   **DISCUSSION**

217   We sought to develop a model of coastal water level that incorporates tidal range as well

218   as wave height to better understand patterns of immersion and emersion on shorelines. The

219   wave-tide model of shoreline water level, composed of two sinusoidal signals (Fig. 1), is simple,

220   highly scalable, and can be used to predict fairly complex patterns in coastal water level. The

221   model predicts the existence of four discrete shoreline benchmarks based upon patterns of

222   submersion and emersion (Fig. 2a-c). These four benchmarks bracket up to three primary

223   physical zones on littoral shores (Fig. 2f): (1) the zone that is continuously emergent at low tide

224   (emergent tidal zone), (2) the zone that is continuously submerged at high tide (submergent tidal

225   zone), and (3) the zone that is continuously washed by waves regardless of tidal level (wave

226 zone). The magnitude of wave height relative to tidal range controls the existence of these zones,

227 and can be used to categorize shores as tide-, co-, or wave-dominated (Fig. 2).

228   The most familiar condition is that of tide-domination, where a large portion of the shore

229 is characterized by tidally induced periods of both emersion and submersion – characteristics that

230 are accurately predicted by our model with an overlap of the emergent and submergent tidal

231 zones (Figs. 2a,d). For the most part, the world's shores have been perceived to be subject to

232 these tide-dominated conditions with only secondary modifications from wave action and other

233 factors (Ricketts et al. 1985). The wave-tide model, however, predicts large portions of the

234 earth's shores are co-dominated and even wave-dominated (Fig. 3), where tidally induced

235 emersion and submersion are spatially disconnected on the high and low shore, respectively (Fig.

236 2). Under co- and wave-dominated conditions, no position on the shore is predicted to

237 experience periods of both emersion and submersion on a tidal schedule, unlike the classic

238 "intertidal" conceptual model. Positions higher on the shore are alternately emerged and washed

239 by waves due to tidal action (emergent tidal zone) while the low shore is alternately submerged

240 and washed by waves (submergent tidal zone) (Fig. 2). During wave-dominated conditions, the

241 mid shore is perpetually washed by waves regardless of tide (wave zone), thus waves modulate

242 the vertical positions of emersion and submersion on shorelines. Importantly, because tidal range

243 is variable and wave height is highly variable, iteration of the model over time and space predicts

244 that the size and position of these zones will be highly variable (Fig. 4).

245

246   **Fine-scale spatial variation**

247   We have demonstrated the application of our model to large temporal and spatial scales,

248 as well as fine temporal scales and midrange spatial scales, but it is also worthwhile to note that

249 our shoreline zonation model can be applied at fine spatial scales of cm to m. Waves and more

250 importantly, wave run-up can be influenced by many factors such as bathymetry, shoreline

251 topography, slope, aspect, porosity, and rugosity. The model's wave height parameter could be

252 replaced with wave run-up parameters and it will reflect differences on fine spatial scales.

253 Varying levels of wave exposure will affect the zonation predicted by the model. For example,

254 shallow reefs can cause waves to break, severely reducing wave height and run-up at the

255 shoreline, relative to that recorded at a wave buoy or coarse satellite imagery. Even within a

256 shore that has fairly consistent wave exposure, there are areas where waves run up higher than

257 others. If a shoreline were outfitted with submersion sensors, the positions of the benchmarks

258 and zones could be estimated. Indeed, fine scale analysis requires fine scale data.

259

260   **Behavior of zones with varying wave exposure and tidal range**

261   Increasing wave exposure is believed to simply elevate and expand the tidally defined

262 zones on the shore – a concept that has remained unchallenged in the literature. However, this

263 behavior is not predicted by the model we present. The position of the emergent tidal zone

264 (vertical bars, Figs. 2d-f) rises but that of the submergent tidal zone (horizontal bars, Figs. 2d-f)

265 sinks on the shore as wave height increases. The wave zone (wavy horizontal bars, Fig. 2f)

266 expands, but the emergent and submergent tidal zones remain the same size as wave height

267 increases. Therefore, increasing wave height while holding tidal range constant displaces the

268 tidal zones both higher and lower on the shore; this leads to the contraction of the region of

269 overlap between the two tidal zones, as well as the emergence and expansion of the wave zone

270 (see progression from Fig. 2d to Fig. 2f). Increasing tidal range, while holding wave height

271 constant, increases the size of emergent and submergent tidal zones which leads to the

272 contraction of the wave zone, and the expansion of the emergent-submergent overlap zone. Thus,

273 the effect of tidal range and wave height fluctuations over time on physical shore zones is

274 predicted to be different than previously envisioned.

275

276   **Physical properties and biological implications of the wave:tide zonation model**

277   At a gross level, the model-predicted zones and their unique physical characteristics can

278 be used to further predict likely sources of stress and disturbance on biological communities.

279 (Fig. 2g-i, Table 1). The pattern and duration of immersion and emersion can have major effects

280 on the foraging of predators and physiological stresses such as temperature, desiccation, and

281 irradiation . As the physical zones move due to temporal variability in wave height and tidal

282 range, conditions are predicted to change, thereby influencing resident shoreline organisms.

283   *Emergent tidal zone*- The emergent tidal zone is characterized by tidally-influenced

284 periods of wave-wash and exposure to air (Fig 2). Therefore, the substratum temperature will be

285 alternately affected by the water, atmosphere and solar irradiation on a tidally defined cycle. The

286 substratum temperature amplitude can be much greater in this zone than the other littoral zones

287 we have defined. The level of drying can be great during low tides, depending on wave splash

288 and humidity, and the level of hydrodynamic force will oscillate from substantial to negligible on

289 a tidally defined cycle. Consequently, the biota residing in the emergent tidal zone will likely

290 contend with the physiological stresses of temperature and desiccation when exposed to the

291 atmosphere and the physical stress of wave force when wetted by the ocean. Terrestrial

292 predators, such as birds, will have access to the emergent tidal zone as the tide recedes, but non-

293 benthic aquatic predators, such as fish, will have limited access to this zone because it will be

294 constantly washed by waves at high water . Benthic marine predators will have to contend with

295 physiological stresses when exposed to the atmosphere and physical stresses when exposed to the

296 aquatic sphere, potentially limiting their efficiency .

297   *Wave zone*- Physiological stresses, such as temperature and desiccation, are minimal in

298 the wave zone because it is constantly washed by waves, and the temperature will be largely

299 affected by the ocean temperature, muting temperature amplitude relative to the emergent tidal

300 zone (Fig. 2). On the other hand, physical stress, in the form of hydrodynamic force caused by

301   wave action, will be constant and the wave zone will receive more wave energy than the

302   emergent or submergent tidal zones. As a result of these conditions, terrestrial and aquatic

303   predators will have to contend with constant wave wash to safely access the wave zone. It is

304   likely that predation will be severely reduced in the wave zone relative to any other littoral zone .

305   *Submergent tidal zone*- Heat and desiccation stresses are negligible in the submergent

306   tidal zone because it is either washed by waves at low tide or completely submerged at high tide,

307   but never fully emergent (Fig. 2). Physical stress will be magnified during periods of wave wash.

308   Terrestrial predators will have little access to the submergent tidal zone, without specific

309   adaptations, but aquatic predators will have easy access during high tides.

310   *Overlapping of the emergent and submergent tidal zones*- These descriptions of the

311   emergent tidal, submergent tidal, and wave zones only apply to co- and wave-dominated

312   conditions. During tide-dominated conditions (Fig 2 a,d,g) the emergent and submergent tidal

313   zones overlap (overlapping vertical and horizontal bars, Fig. 2d). The result of the overlap

314   between the zones is that the area is characterized by discrete tidally defined periods of exposure

315   to the atmosphere, wave wash, and submergence – the conditions traditionally ascribed to a

316   classic "intertidal" zone (Fig 2. g). Biota residing in this area of overlap are subject to

317   physiological stresses (temperature, desiccation, and irradiation) during low water, are submerged

318   at high water, and are exposed to physical stress in the wave wash at some point between high

319   and low water. Terrestrial and aquatic predators have windows of foraging opportunity at low

320   and high water, respectively, but are restricted during the periodic wave wash events with the

321   tidal rise and fall .

322   The non-overlapping regions of the emergent tidal (vertical bars, Fig. 2d) and submergent

323   tidal zones (horizontal bars, Fig. 2d) share properties with those zones under co- and wave-

324   dominated conditions, but the periods of exposure to the atmosphere and submergence in the

325   emergent and submergent tidal zones, respectively, are long relative to the periods of wave wash.

326 Thus, physical stress caused by waves will be reduced to shorter periods of time in both the

327 emergent and submergent tidal zones under tide-dominated conditions. Physiological stress is

328 potentially great and predation by swimming aquatic predators should be limited in the non-

329 overlapping portion of the emergent tidal zone. In contrast, physiological stress will be minimal

330 and access by aquatic predators will only be limited only during short periods of wave wash in

331 the non-overlapping portion of the submergent tidal zone.

332

333   **Consequences of variability in tidal range and wave height**

334   While the general qualitative conditions we attributed to the physical zones on littoral

335 shores are predicted to remain relatively constant over time, significant variation in both tidal

336 range and wave height is expected within sites as well as among them. This variability within

337 sites can lead to variation in the position and existence of these zones on a variety of time scales

338 (Figs. 2g-i). Against this backdrop of long-term average conditions, any given position on a

339 shore can be characterized by a temporary profile of another of the physical zones we have

340 described. Given that stresses and disturbances are often the result of uncommon events, rare

341 departures from average physical conditions are likely to be events of extreme stress and

342 disturbance. For example, ~0.5 m above MLLW at Mokapu, HI is almost always predicted to be

343 in the wave zone (below B_2 and above B_3, Fig. 2i), but is occasionally in the lower emergent tidal

344 zone. On these rare occasions where 0.5 m is in the emergent tidal zone, physical stress due to

345 constant wave wash will be alleviated but physiological stress due to temperature, desiccation,

346 and solar radiation, as well as foraging by terrestrial predators are much more likely to impact the

347 biota.

348   In Portland, ME, ~1.5 m above MLLW is predicted to be typically in the overlap of the

349 emergent and submergent tidal zones, but in approximately 23 discrete high-wave events it is

350 solely in the upper submergent tidal zone or the wave zone (Fig. 2g). During these rare events,

351 physiological stress is expected to be greatly reduced, but physical stress is expected to be

352 elevated. Overall, both the average long-term conditions and the impact of rare events are

353 expected to be important determinants of community structure. Our model aids in the

354 identification of both the long term average conditions and these rare stress/disturbance events

355 and facilitates the generation of specific predictions of how each will affect resident biota at

356 specific positions on the shore.

357   When considering the additional complexities of the effects of bathymetry on wave height

358 and the effects of shore topography, slope, porosity, effective fetch, and rugosity on wave run-up ,

359 it is easy to foresee that the model-predicted environmental conditions, based solely on coarse

360 scale measurements of wave height and tidal range, may not exactly match the actual conditions

361 at particular positions on the shore. The model is only as good as the data driving it, thus fine

362 scale tests of the model must include fine scale wave run-up and tidal data (e.g., Harley &

363 Helmuth 2003; Burrows et al. 2008). The power of the model lies in its scalability and its ability

364 to identify transitions from tide- to co- to wave-domination, define typical conditions and

365 significant departures from the norm, and make general predictions about the stresses affecting

366 the biotic processes operating on any given shore.

367

368   **Relevance of a physical zonation model**

369   The use of physical zonation as a tool to better understand ecological processes on littoral

370 shores has been refuted by Underwood who demonstrated there are no sharp changes in

371 inundation patterns due to tidal ebb and flow, and thus, no zonation. Our model of shoreline

372 water level and physical zonation is predicated on the smooth sinusoidal behavior of tidal ebb and

373 flow, and is thus wholly consistent with the findings of Underwood (1978). Yet, we identify

374 critical, physically-defined benchmarks on the shore when considering wave action as well as

375 tidal fluctuation. We further agree with Underwood (1978) that particular species are not likely

376   to be strictly limited within or by these zones. We propose, however, that the conditions

377   associated with these zones and their positions (as determined by the ratio of wave height to tidal

378   range) will have prominent effects on physical and physiological stress and disturbance

379   experienced by shoreline populations. The differential stresses in each zone will impact

380   prominent biotic interactions such as predation, competition, and facilitation . Consequently, our

381   model of physical zonation is an effective tool that can inform and facilitate our understanding of

382   physical processes operating on littoral shores, and is a fundamental advancement beyond the

383   classic intertidal concept.

384

385   **Conclusion**

386   Our model of coastal water level indicates that waves do not simply expand and elevate

387   physical littoral zones that exist in the absence of waves. Rather, waves interact with tides to

388   create up to three distinct physical zones (emergent tidal zone, wave zone, submergent tidal zone)

389   that are characterized by unique submersion-emersion and hydrodynamic characteristics. The

390   differential properties of these zones and the variability in their existence, overlap, and positions

391   leads to specific and falsifiable hypotheses regarding differential regimes of physical and

392   physiological and stress and disturbance for organismal shoreline populations. What is more, our

393   model of littoral zonation is completely consistent with the findings of previous studies that have

394   argued against the existence of intertidal zonation (Underwood 1978, Benedetti-Cecchi & Cinelli

395   1997), and is not hampered by a complete dependence on tidal patterns, geographic location, or

396   the biological definition of zones. Thus, this model provides a unifying framework to better

397   understand the physical littoral habitat and biotic stress regimes on shores, whether they are

398   temperate, tropical, marine, or lentic.

399

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Figure 1

Model of shoreline water level over a single tidal cycle.

Representation of water level incorporating (a) only tidal range, (b) only wave height, and (c) both tidal range and wave height. The tidal amplitude (A_T), tidal period (P_T), wave amplitude (A_W), and wave period (P_W) are noted.
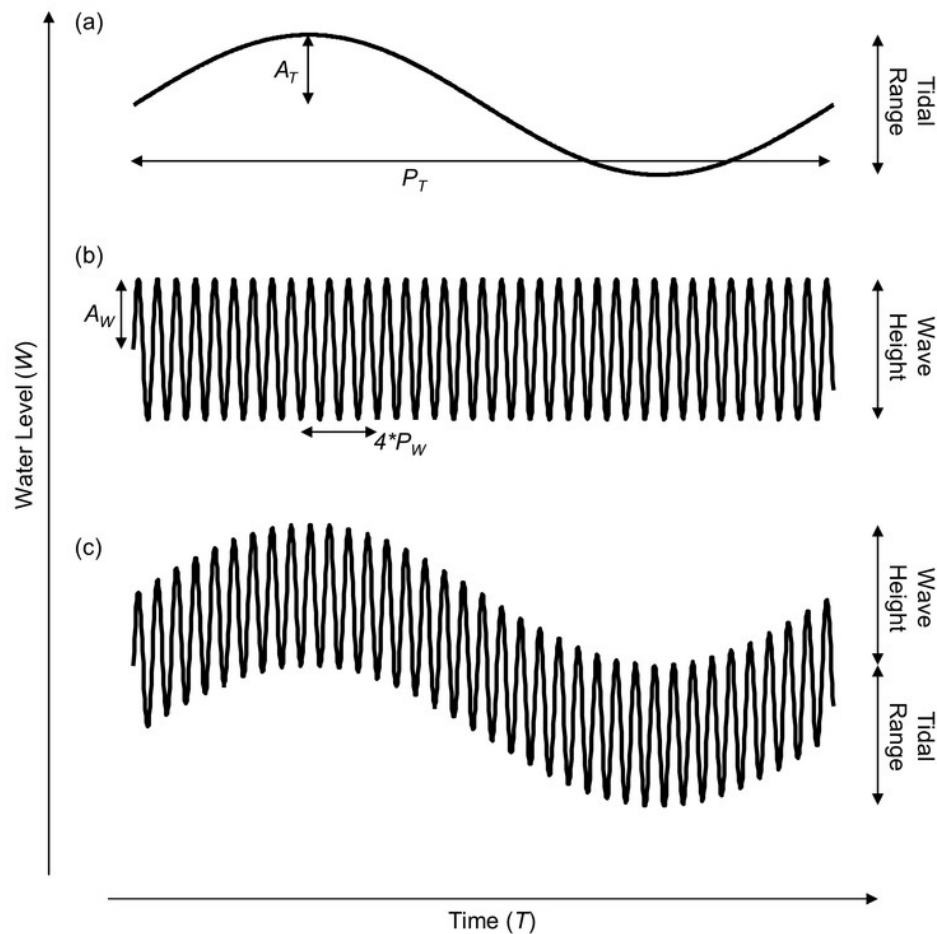
Figure 2

Wave-tide model of shoreline water level.

Using three ratios of wave height to tidal range: 0.1:1 (a, c, g), 1:1 (b, e, h), and 2:1 (c, f, i), we show shoreline water level and shoreline benchmarks. The four shoreline benchmarks predicted by the model (B1-B4) are demarcated by colored lines and the zones they bracket are shown in panels d-f. Relative wave energy, continuous emersion time and submersion time are diagramed in the conceptual models in panels g-i.
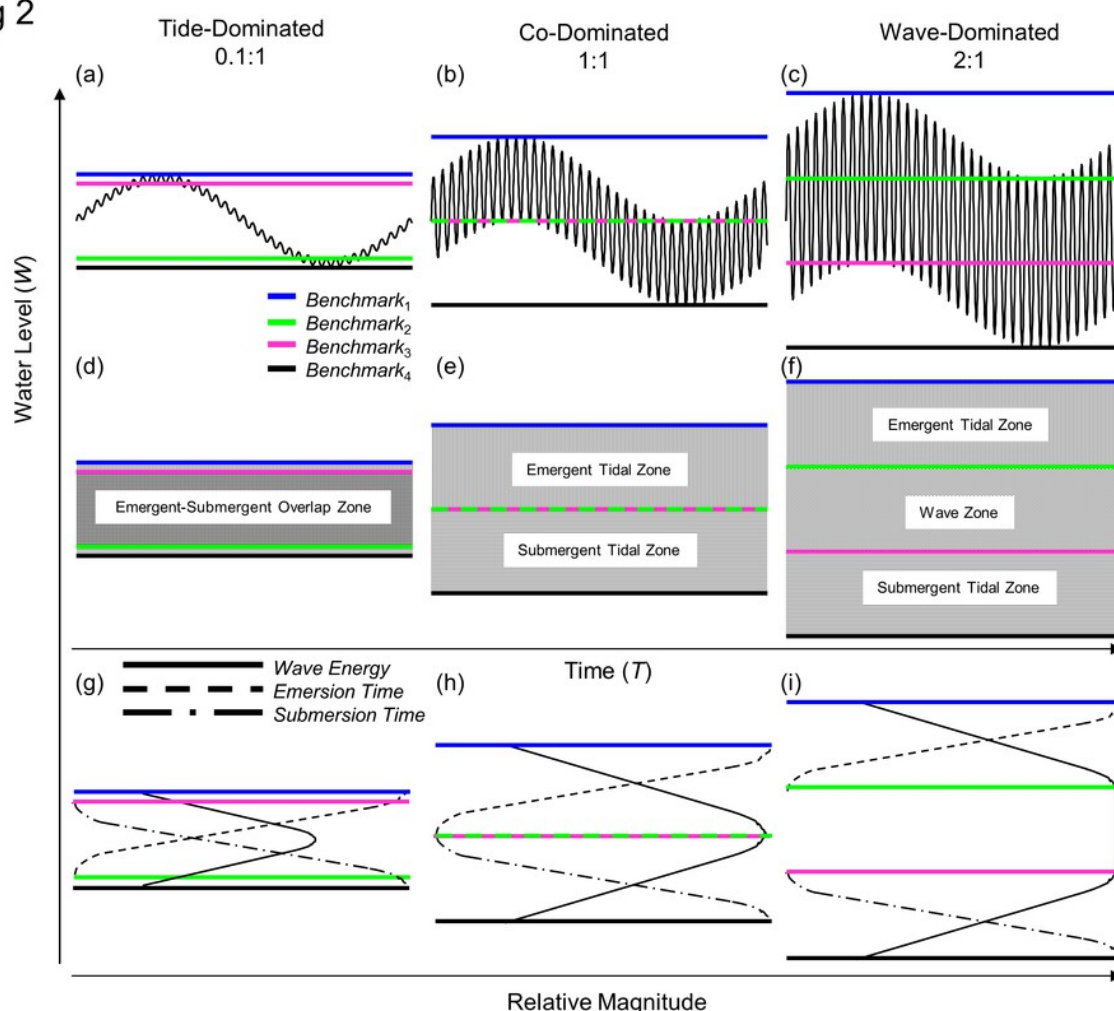
Figure 3

Global map classifying shorelines according to relative wave and tidal ranges.

(a) Shorelines classified as tide-dominated (mean diurnal tidal range >> mean significant wave height), co-dominated (mean diurnal tidal range ≈ mean significant wave height), and wave-dominated (mean significant wave height >> mean diurnal tidal range. (b) Ocean area color-coded by the ratio of wave height to tidal range. The locations of the sites featured in this study are indicated with stars – from left to right, Mokapu, Hawaii; Humboldt, California; and Portland Maine.
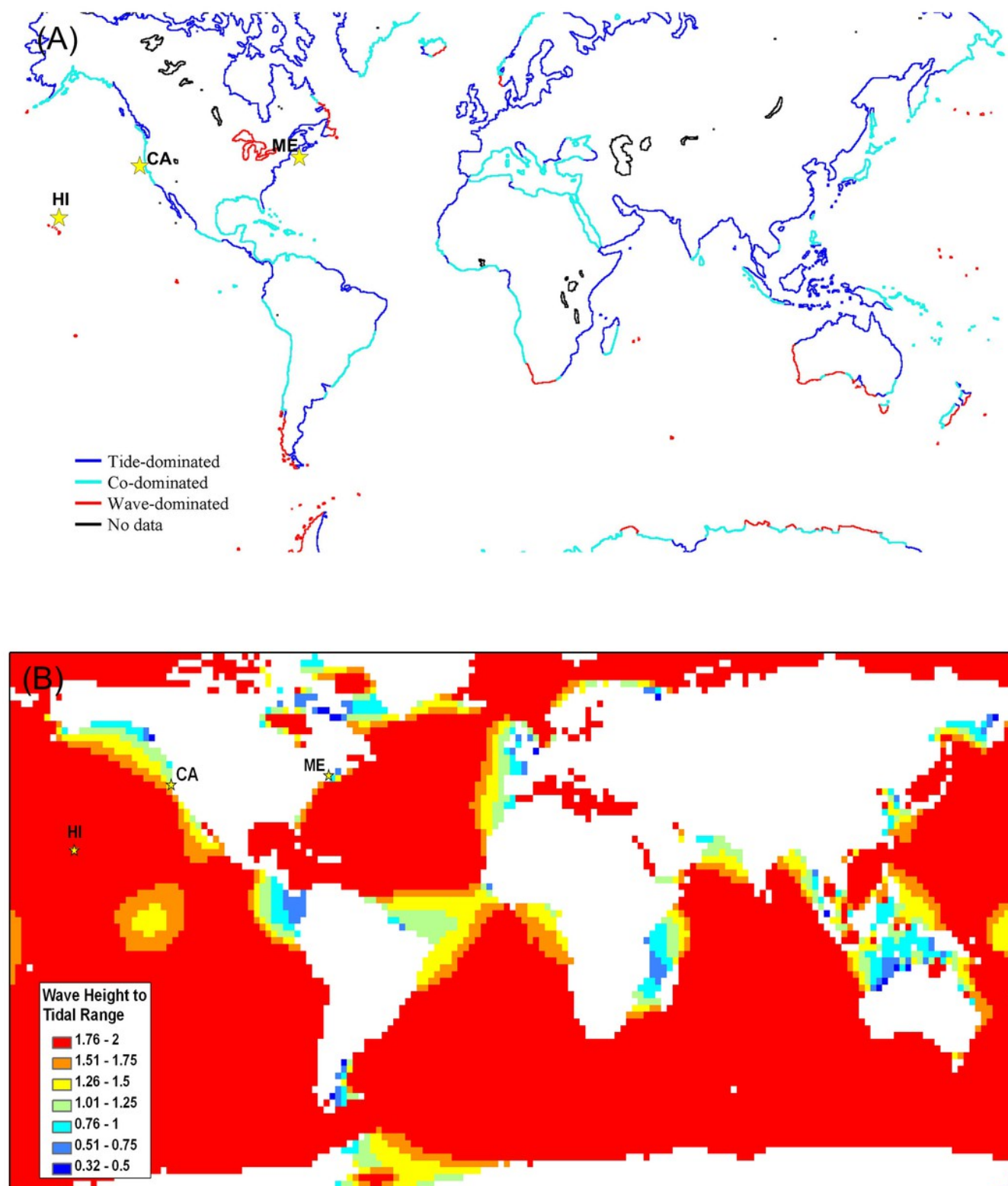
Fig 3

Figure 4

Coastal water levels and physical zones across three representative sites.

Model of coastal water level (Equation 3, panels a-c), derived benchmarks and physical zones (Equations 4-7, panels d-i), and histograms of the hourly frequency of the ratio of wave height to tidal range (panels j-l) applied to three representative wave-exposed sites along a continuum from tide- to wave-domination (Portland, ME; Humboldt, CA; and Mokapu, HI respectively). Panels a-c display the water level during one tidal cycle (12.2 h oscillation period) from MHHW to MLLW at the yearly mean significant wave height (shorter oscillation period) plotted against time. Panels d-f display the physical zones we derive from our model of coastal water level. Panels g-i show the hourly determination of benchmark 1(blue line), benchmark 2 (green line), benchmark 3 (fuscia line), and benchmark 4 (black line), plotted against time from June 2005 to June 2006. Note that the rank positions of Benchmark 2 and Benchmark 3 switch from panels a, d, and g to panels c, f, and i.
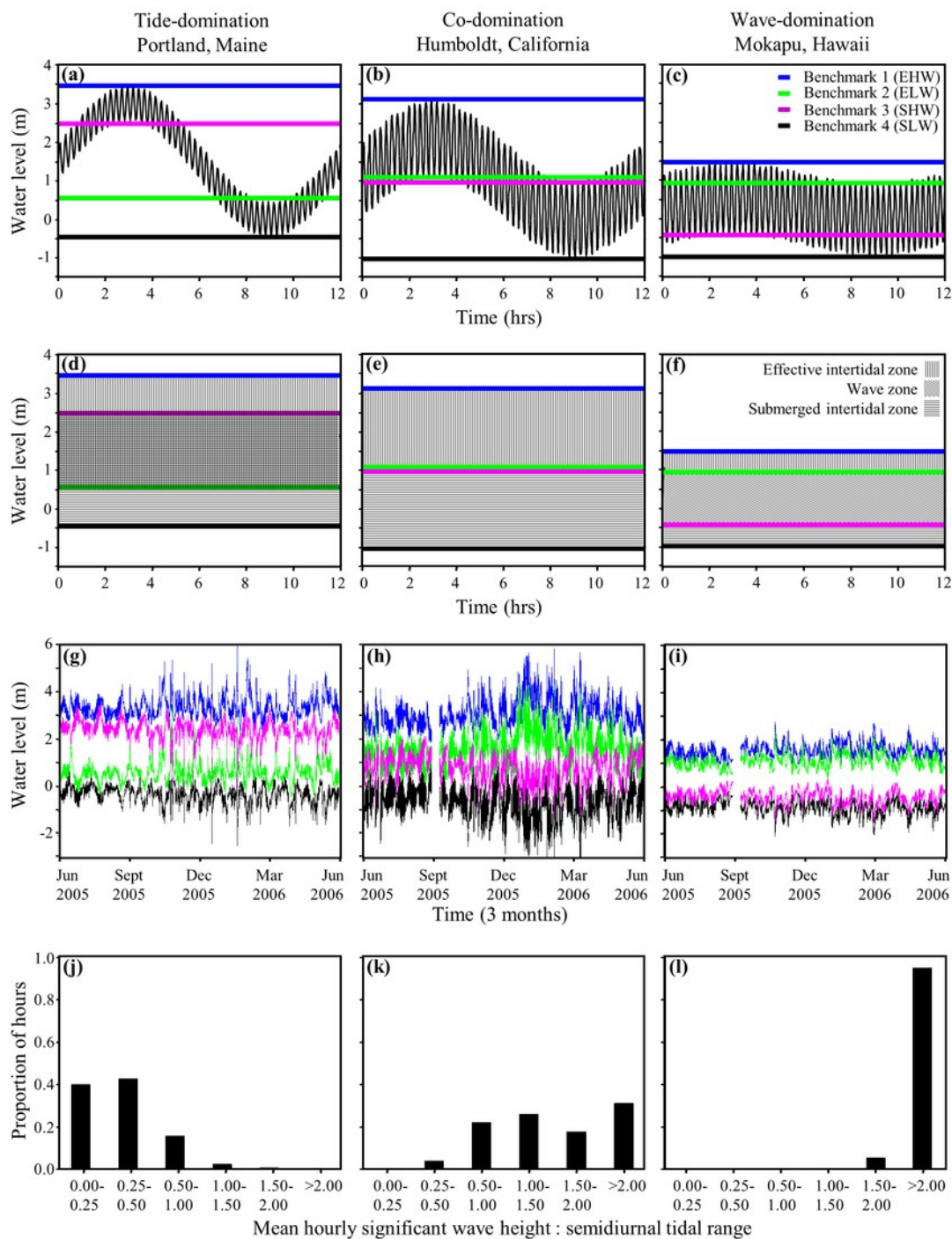
Fig 4

Predominant physical conditions and their corresponding biological consequences for each of the zones predicted by the wave:tide zonation model.

Characterizations of predominant physical conditions and their biological consequences based on the assumption that the shores are equally wave-exposed. The predominant physical conditions and their corresponding biological consequences are ranked with zero to four "x" to indicate the magnitude of effect for each category column.

Habitat	Wave:Tide Regime			Physical conditions					Biological consequences				
	Tide Dominated	Co-dominated	Wave dominated	Tidal Emersion	Tidal Submersion	Wave wash	Wave force	Relative wave energy	Physiological stress	Physical stress	Benthic Predation efficiency	Pelagic Predation efficiency	Terrestrial Predation efficiency
Emergent tidal zone		Present	Present	XXXX		XX	XXXX	XX	XXXX	XX	XX		XXXX
Wave zone			Present			XXXX	XXXX	XXXX		XXXX	X	X	X
Submergent tidal zone		Present	Present		XXXX	XX	XXXX	XX		XX	XXXX	XXXX	
Emergent-submergent overlap zone	Present			XXXX	XXXX	X	XXXX	X	XXXX	X	XXXX	XXXX	XXXX

1   1