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7   Testing the Intermittent Upwelling Hypothesis: Upwelling, Downwelling, and Subsidies to the

8                                   Intertidal Zone

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23  Running Head: Testing Intermittent Upwelling Hypothesis

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26  **Abstract**

27  The Intermittent Upwelling Hypothesis (IUH) posits that subsidies of larvae and phytoplankton

28  to intertidal communities should vary unimodally along a gradient of upwelling from persistent

29  upwelling to persistent downwelling with most subsidies occurring where upwelling is of

30    intermediate strength and intermittent. Furthermore, the hypothesis states that larvae and

31    phytoplankton are transported far offshore by strong, persistent upwelling and fail to subsidize

32    nearshore communities, whereas weak upwelling or downwelling reduces nutrients for

33    phytoplankton production limiting food for larvae and nearshore communities. We review

34    studies conducted at sea and onshore and reanalyze published data to test the IUH and evaluate

35    alternative hypotheses. To test the hypothesis, we examine five predictions that must hold if the

36    IUH is true. 1) *Larvae should inhabit the surface Ekman layer where they are transported*

37    *offshore during upwelling.* Larvae of many intertidal taxa occur deeper in the water column

38    where currents flow shoreward during upwelling. 2) *Larvae of nearshore species should occur*

39    *farther offshore during upwelling than during relaxation or downwelling.* Larvae of many

40    nearshore species remain within several kilometers of shore during both conditions. 3) *Larval*

41    *settlement in intertidal communities should be lower during upwelling than relaxation or*

42    *downwelling.* Daily larval settlement has not observed to be higher during relaxation or

43    downwelling events; settlement has most often been seen to vary with the fortnightly tidal cycle

44    likely due to onshore larval transport by internal tides. 4) *Larval settlement and recruitment in*

45    *intertidal communities should be lower in areas of strong, persistent upwelling than where*

46    *upwelling is weaker and less persistent.* Recruitment of mussels and barnacles to artificial and

47    natural substrates did not vary with the strength of upwelling, but did vary inversely with two

48    measures of desiccation potential, and directly with indicators of surfzone hydrodynamics; larval

49    recruitment was higher where surf zones were more dissipative with rip currents. 5)

50    *Phytoplankton subsidies to nearshore communities should be highest where upwelling is*

51    *moderate and intermittent.* Like larval subsidies, phytoplankton subsidies varied spatially with

52    surfzone hydrodynamics rather than upwelling. This reconsideration of the evidence for the IUH

53    finds the hypothesis unsupported.

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56    **Key Words:** surf zone, barnacles, settlement, subsidies, intertidal, recruitment, mussels,

57    hydrodynamics, dessication

58

59    **Introduction**

60      The importance of larval settlement and postsettlement mortality to the dynamics of

61   marine populations and communities has been investigated for over a century (Morgan 2001).

62   Along the west coast of the USA, a considerable body of research demonstrated the importance

63   in the Pacific Northwest of postsettlement mortality in regulating rocky shore communities. In

64   contrast, in a highly influential paper, Roughgarden et al. (1988) proposed that low larval

65   settlement regulated intertidal communities in California. They hypothesized that larvae

66   developing in strong, persistent upwelling off California are swept so far offshore by surface

67   currents that few of them return to shore to settle. Consequently, populations are recruitment

68   limited in the strong, persistent upwelling along the California coast, whereas an abundant

69   supply of larvae in the weaker, less persistent upwelling in the Pacific Northwest results in

70   postsettlement density-dependent regulation of populations

71      A corollary to this hypothesis was that the alongshore distribution of upwelling also

72   affects the delivery of phytoplankton food subsidies to the intertidal zone (Menge and Menge

73   2013). Wind-driven coastal upwelling draws nutrient rich waters from depth to the euphotic zone

74   close to the coast leading to high phytoplankton productivity, standing stocks and subsidies to

75   intertidal communities. However, if upwelling is strong and persistent, blooms are transported

76   far from shore (Botsford et al. 2006), and subsidies of phytoplankton to the intertidal

77   communities are hypothesized to be low. During relaxation of upwelling or downwelling events,

78   the influx of nutrients is low leading to lower phytoplankton productivity, standing stocks and

79   subsidies to intertidal communities. Thus, phytoplankton subsidies to the shore should be higher

80   in regions of moderate intermittent upwelling than where upwelling or downwelling are strong

81   and persistent.

82      Critical tests of the effects of upwelling on larval recruitment have been conducted at sea

83   as well as onshore, and we review this literature to reconsider the importance of latitudinal

84   variation in upwelling on larval settlement and recruitment and phytoplankton subsidies to rocky

85   shore populations and communities. As well as reviewing published research, we reanalyzed

86   some published data to evaluate new explanations for results formerly attributed to upwelling.

87   The hypothesis originated over 30 years ago with much of the supporting evidence coming from

88   studies conducted along the West Coast of North America, and consequently, we have focused

89   on the California Current Large Marine Ecosystem (CCLME).  We address five predictions or

90   expectations of the Intermittent Upwelling Hypothesis that must hold if the hypothesis is true.

91   We selected these five predictions because they are both key tests of the hypothesis and
92   published data are available to actually make the tests. The first two predictions deal with the
93   pelagic phase of larval dispersal and the last three with the delivery of subsidies (larval settlers
94   and phytoplankton) to the shore and their subsequent recruitment. None of the predictions of the
95   IUH was supported by the evidence.

96

97   ***Prediction 1: Larvae spend most of their time in the surface Ekman layer where wind-driven***
98   ***upwelling currents transport them offshore***.

99            When upwelling favorable winds (from the north in the CCLME) blow parallel to shore,
100   due to the Coriolis effect, flow in the surface Ekman layer (upper 10 to 20 m) is downwind and
101   offshore causing a drop in sea level at the coast and, to compensate, water from below the
102   Ekman layer flows onshore (Mann and Lazier 1991). During downwelling-favorable winds
103   (from the south in the CCLME), the flow regime is reversed. Given this flow regime, larvae in
104   the surface Ekman layer will be transported offshore during upwelling and back toward the shore
105   during relaxation or downwelling, and larvae below the Ekman layer will experience transport in
106   the opposite directions.
107            For their 1988 paper, Roughgarden et al. analyzed samples from oblique zooplankton
108   tows collected by CalCOFI (California Cooperative Fisheries Investigation) as part of a long-
109   term study of variations in sardine and anchovy populations in the CCLME; oblique plankton
110   tows, however, provided no indication of the depth inhabited by larvae caught in the tows.  A
111   number of researchers have subsequently collected vertically stratified samples from throughout
112   the water column to test this hypothesis (see for example Shanks and Shearman 2009, Morgan et
113   al. 2009b). These studies determined that larvae of most nearshore species occur below the
114   surface Ekman layer. For example, Shanks and Shearman (2009) found that the larvae of all
115   intertidal barnacles and all stages of these barnacles were caught deeper than the Ekman layer;
116   during upwelling they inhabited the deeper upwelled water that was flowing shoreward and
117   during downwelling they were found deeper as well and may be transported offshore. Morgan et
118   al. (2009b) showed that larvae of most of the 46 species of crustaceans collected by their
119   sampling occurred deeper in the water column throughout the day or rose to the surface at night
120   after strong afternoon upwelling winds subsided (Morgan and Fisher 2010). There were larvae of
121   some species that did occupy the surface layer and they were transported farther offshore before

122  returning to the nearshore late in development. Larvae of most nearshore species of invertebrates

123  do not spend most of their time in the surface Ekman layer, and in fact, many spend little time in

124  the surface Ekman layer.  Similar results have been found by Bartilotti et al. (2014) in the

125  upwelling regime of the Iberian Peninsula. These results are not consistent with Prediction 1.

126

127  ***Prediction 2. Larvae of nearshore species should occur farther offshore during upwelling than***

128  ***during relaxation or downwelling.***

129       As support for their hypothesis, Roughgarden et al. (1988), using the CalCOFI samples,

130  correlated the most seaward extent of barnacle larvae from shore with the strength of upwelling

131  and found that larvae tended to occur farthest offshore during strong upwelling. Anchovies and

132  sardines in the CCLME tend to spawn well offshore, and the CalCOFI samples analyzed by

133  Roughgarden et al. were designed to capture these larvae. As a consequence, the most nearshore

134  station sampled by CalCOFI tended to be 5 nm (9 km) offshore (Roughgarden et al. 1988).

135  Intertidal barnacle larvae are released nearshore in the coastal boundary layer, where cross-shore

136  currents are generally slow due to friction with the bottom and shore (Nickols et al. 2012,

137  Nickols et al. 2013); given current speeds in the coastal boundary layer, it should take days for

138  larvae to be transported far enough offshore to be caught during CalCOFI sampling. Perhaps the

139  CalCOFI samples were collected so far offshore that they actually missed the bulk of the

140  barnacle larvae. Because the cross-shelf distribution and abundance of barnacle larvae was not

141  determined, their samples may represent the few unfortunate individuals that were larval

142  wastage.

143       Subsequent studies filled this gap by sampling at stations from several hundred meters to

144  70 km offshore in the CCLME (Morgan et al. 2009a, Morgan et al. 2009b, Shanks and Shearman

145  2009, Morgan 2014), other upwelling regimes (Poulin et al. 2002, Bartilottii et al. 2014, Morgan

146  2014) and elsewhere (Shanks et al. 2002, Shanks et al. 2003, Shanks and Brink 2005). These

147  studies determined that the larvae of barnacles and many other nearshore species of invertebrates

148  remain close to shore rather than being transported offshore by strong upwelling currents. For

149  example, Shanks and Shearman (2009) found that all larval stages of all the intertidal barnacles

150  were found close to shore, within several km of shore, and that their average distance offshore

151  (generally < 2 km) did not vary with upwelling or downwelling. Similar results were obtained for

152  barnacles as well as many other species of nearshore crustaceans in other studies (Morgan et al.

153   2009a, Morgan et al. 2009b, Fisher et al. 2014). Moreover, these latter studies found that larvae

154   of species developing over the mid or outer continental shelf did not occur farther offshore

155   during strong upwelling conditions either.

156        The conclusion from these studies is that upwelling does not sweep larvae of many,

157   perhaps most, intertidal species far offshore. By avoiding the surface Ekman layer, larvae of

158   most species are not carried offshore by upwelling but, instead, remain within several kilometers

159   of shore throughout their pelagic development. These results are not consistent with Prediction 2.

160        The dispersal of those larvae of intertidal and shallow subtidal species that remain within

161   several kilometers of shore is under the influence of nearshore hydrodynamics and this leads to a

162   number of consequences. 1) During upwelling, the warm, lower density surface layer of the

163   ocean is pushed offshore and is replaced by cold, denser upwelled water. These two water

164   masses meet forming an upwelling front between the cold upwelled water onshore and the warm

165   surface water transported offshore around 10 to 15 km from shore (Mann and Lazier 1991). As

166   the upwelling season progresses in the CCLME, large eddies, known as jets and squirts, develop

167   in the California Current, which transport continental shelf water far seaward (Korso and Huyer

168   1986, Strub et al. 1991, Strub and James 2000). Current drifters set seaward of the upwelling

169   front tend to be entrained in these jets and squirts and are carried far from shore (Barth and Smith

170   1998, Barth et al. 2000), as would larvae of many rockfish species that develop beyond the

171   upwelling front (Fiedler 1986, Haury et al. 1986). In contrast, drifters set landward of the

172   upwelling front tend to be carried back toward shore where they often run aground (Barth and

173   Smith 1998, Barth et al. 2000). Because larvae of most nearshore taxa complete development

174   well landward of the upwelling front, they should seldom encounter jets and squirts and instead

175   be transported onshore like the drifters set landward of the upwelling front (Austin and Barth

176   2002). 2) During upwelling, the most rapid alongshore current is within the upwelling jet

177   associated with the upwelling front, but the jet does not affect the rate of alongshore larval

178   transport for the many intertidal species that complete their pelagic development in waters

179   kilometers landward of the jet (Kosro et al. 1997). 3) Larvae of intertidal and nearshore species

180   are released in the coastal boundary layer, retarding seaward and alongshore dispersal (Morgan

181   et al. 2009a, Nickols et al. 2013, Hameed et al. 2016). 4) During the upwelling season, roughly

182   every week or two winds shift from upwelling to downwelling favorable (Mann and Lazier

183   1991). During upwelling favorable winds in the CCLME, nearshore currents flow to the south,

184    and during downwelling, they reverse and flow north (in the Southern Hemisphere wind driven

185    upwelling systems currents are reversed). Larvae of most intertidal fishes and benthic

186    invertebrates that spawn during the upwelling season are likely transported alongshore both north

187    and south as wind reversals occur during their four to six week planktonic phase (average 45

188    days) (Shanks and Eckert 2005).  By capturing this variation in current direction, larvae may

189    tend to remain closer to their point of release (Largier 2003).

190         How do slowly swimming larvae remaining below the surface Ekman layer stay roughly

191    the same distance offshore rather than being transported shoreward during upwelling and

192    seaward during downwelling? As water shoals close to shore, the baroclinic currents generated

193    by Ekman transport are suppressed (Austin and Lentz 2002) limiting cross-shelf transport of

194    larvae. Water within the coastal boundary layer is, however, exchanged during wind reversals

195    (Csanady 1974), which should transport larvae embedded in the water mass along with it if

196    larvae behaved as passive particles. Larvae do not remain attached to a water mass indicating

197    that they are far from passive. Shanks and Brink (2005) repeatedly sampled a transect

198    perpendicular to shore for over a week while winds shifted from upwelling to downwelling and

199    back to upwelling. The water mass adjacent to shore was exchanged with each wind shift,

200    whereas, slowly swimming bivalve larvae of nearshore taxa remained roughly the same distance

201    offshore rather than tracking water masses as they were exchanged. Although these observations

202    were made on the east coast of North America, which is not a predominantly wind-driven

203    upwelling system, the horizontal baroclinic cross-shelf currents generated by upwelling were still

204    at least an order of magnitude faster than larval swimming speeds (Shanks and Brink 2005). The

205    authors hypothesized that by swimming vertically in the much slower downwelling (upwelling)

206    currents converging (diverging) against the shore, larvae may have been able to maintain their

207    position close to shore despite the exchange of water masses. A similar mechanism may be

208    occurring in wind-driven upwelling systems associated with eastern boundary currents like the

209    California Current.

210    ***Prediction 3. Daily settlement of larvae in the intertidal zone should be lower during upwelling***

211    ***and higher during downwelling conditions.***

212         Upwelling surface currents were hypothesized to cause enough offshore transport for

213    larvae to be lost to coastal populations resulting in low settlement at the shore, whereas the

214    reverse is hypothesized to occur during relaxation from upwelling or downwelling conditions

215    (Farrell et al. 1991, Roughgarden et al. 1991). There are two mechanisms that may transport

216    larvae shoreward during a downwelling or upwelling relaxation event. As described above, a

217    front is formed offshore separating the cold upwelled water from the warm surface water that has

218    been pushed offshore. Following an upwelling event (e.g., onset of downwelling or upwelling

219    relaxation), the cool upwelled water sinks back to a stable vertical distribution and the warm

220    water beyond the upwelling front flows back toward shore as a density current (Shanks et al.

221    2000). If prior to the commencement of new upwelling, larvae are released into the warm surface

222    water and remain there, they will be transported offshore during subsequent upwelling and they

223    will occur in the lens of warm water on the seaward side of the upwelling front. With relaxation

224    of upwelling-favorable winds, they will be transported back toward shore by the density current.

225    When this lens of warm water contacts shore and remains in contact with the shore, settlement in

226    intertidal communities should be higher.  The warm water flowing back toward shore takes the

227    form of a moving convergent front with surface flow toward the front from both the warm and

228    cool water sides of the front (Shanks et al. 2000). Larvae carried into the convergent front can be

229    transported shoreward by the moving convergence (Shanks et al. 2000). This will also lead to

230    higher settlement at the shore during downwelling events, but the settlement should appear as a

231    brief pulse as the front arrives onshore.

232        A number of studies have measured barnacle settlement and the abundance of crab

233    megalopae at the shore daily or every two days and results are not consistent with Prediction 3

234    (Shanks 1983, Shanks 1986, Farrell et al. 1991, Pineda 1991, 1994, Shanks 1998, Shanks 2006,

235    Roegner et al. 2007, Shanks 2009a, b, Shanks et al. 2014). These studies consistently found that

236    the delivery of settlers tends to occur in brief pulses of one to several days, and the pulses are

237    cross-correlated with the tidal amplitude cycle of spring to neap tides. The fortnightly periodicity

238    in settlement is most likely due to onshore transport by the internal tides either by moving

239    convergences over these internal waves or by internal bores generated by breaking internal

240    waves (Shanks 1983, Pineda 1991). Contrary to expectations, larval settlement was not related to

241    relaxation events; it was actually higher during upwelling, but the positive effect of upwelling

242    winds on settlement was only apparent after the much stronger fortnightly tidal effect had been

243    removed from the time series (Shanks 2009a). For the purpose of this review of the IUH, the

244    important point is not that onshore transport of larvae often appears to be due to tidally generated

245    internal waves, rather it is that when settlement and larval abundance have been measured daily,

246    there is no evidence for the hypothesized higher settlement during downwelling and relaxation

247    events.

248         An apparent exception to these observations was a paper by Farrell et al. (1991) in which

249    they interpreted their data to indicate that barnacle settlement was higher following a

250    downwelling event, although they did not statistically test this effect. Subsequent time-series

251    analysis revealed that there was a clear fortnightly effect of the spring-neap tidal amplitude cycle

252    in this data set as well and no effect of upwelling and downwelling (Shanks 2009a).

253         At a coastal site near Duck, North Carolina, Shanks et al. (2000) sampled an upwelling

254    front propagating toward shore during an upwelling relaxation event. The front formed a moving

255    convergence zone that transported blue crab (*Callinectes sapidus*) megalopae toward shore as

256    predicted by the IUH. Daily abundance of blue crab megalopae sampled during the same period

257    and at the same sample site, however, varied with the fortnightly tidal cycle (Shanks 1998)

258    suggesting the megalopae were regularly transported shoreward by the internal tides. Indeed,

259    observations off Beaufort, North Carolina demonstrated that moving convergences generated by

260    internal waves transported blue crab megalopae as well as a number of other larval types

261    shoreward (Shanks 1988). We conclude from these studies that moving convergences generated

262    by any mechanism can transport larvae (Shanks et al. 2000). However, over the continental shelf,

263    moving convergences are more frequently generated by the internal tides than relaxation events,

264    and this mode of onshore transport shows up in time series of daily settlement and abundance of

265    larvae as a fortnightly signal.

266         Although the IUH suggests that peaks in the abundance of settlers at the shore should

267    occur during downwelling and relaxation events, researchers have consistently found that

268    abundance varies with a fortnightly periodicity related to the tidal amplitude cycle. Abundance

269    peaks related to downwelling or upwelling relaxation events were not observed. Thus, Prediction

270    3 is not supported.

271    ***Prediction 4. Where upwelling is strong and persistent, settlement and recruitment in the***

272    ***intertidal zone should be lower than where upwelling is less persistent***.

273         The rational behind this prediction is that where upwelling is strong and persistent, larvae

274    of intertidal organisms are pushed out to sea and lost to the population; but where upwelling is

275    weaker and less persistent, larvae are transported shoreward and settle during more frequent

276    relaxation conditions (Roughgarden et al. 1988). The strength and persistence of upwelling

277 changes with latitude (Checkley and Barth 2009), and therefore, so might larval recruitment to

278 adult populations (Roughgarden et al. 1988). Where or when larval supply is high, recruitment to

279 adult populations will be high (Menge and Menge 2013). Alongshore variation in the apparent

280 recruitment of barnacles and mussels, which appears to be related to alongshore variation in

281 upwelling, has been presented as amongst the strongest evidence supporting the IUH (reviewed

282 in Menge and Menge 2013). Several papers have compared latitudinal variation in the

283 recruitment of barnacles or mussels to the distribution of upwelling within the CCLME

284 (Connolly et al. 2001, Menge et al. 2004, Broitman et al. 2008) as well as along the coast of

285 Chile (Navarrete et al. 2005). The consensus is that where upwelling is strong and persistent

286 recruitment is lower than in areas of weak upwelling.

287        Although the recruitment data do appear to support the IUH, there are problems both with

288 the data and with the interpretation of the data that warrant reconsideration. As described above,

289 the vertical and cross-shelf distribution of larvae do not match the predictions of the IUH. Larvae

290 were not in the surface Ekman layer and upwelling did not transport them offshore; instead most

291 larvae were found below the surface Ekman layer and remained within several kilometers of

292 shore. In addition, when settlement was measured daily, higher settlement rates did not occur

293 during downwelling events, but rather settlement rate followed a fortnightly pattern suggestive of

294 transport to shore by the internal tides. Hence, the underlying rational used to explain the

295 potential effect of upwelling intensity on alongshore variation in recruitment is not supported by

296 empirical data collected at sea and onshore.

297        Much of the data on recruitment of barnacles has been collected using Safety-Walk

298 plates, Plexiglas plates covered with non-skid Safety-Walk® tape (reviewed in Menge and

299 Menge 2013). The rough surface of the tape appears to be an ideal settlement surface for cyprids

300 that prefer rugose substrates, but unfortunately, the tape heats up rapidly in the sun reaching

301 surface temperatures (e.g., 40 to 50 ℃) lethal to settled cyprids in tens of minutes (Shanks

302 2009b). Despite this potential artifact, Broitman et al. (2008) found significant correlations

303 between recruitment and cyprid settlers on recovered Safety-Walk plates. Although the heating

304 problem may have been over emphasized (Shanks 2009b), recruitment data using Safety-Walk

305 plates should be interpreted cautiously because solar energy varies with latitude as does the

306 typical coastal weather at a site, including fog often associated with upwelling.

307　　　　　Investigators recently have begun to examine the potential effects of surfzone

308　hydrodynamics on the delivery of larvae and phytoplankton subsidies to shore (Rilov et al. 2008,

309　Shanks et al. 2010, Morgan et al. 2016, Shanks et al. 2016, Morgan et al. 2017a, Shanks et al.

310　2017b, Shanks et al. 2017c). Surf zones vary from reflective (steeply angled shores with narrow

311　surf zones) to more dissipative (gently sloping shores with wide surf zones). Surfzone

312　hydrodynamics can both limit the onshore migration of larvae from the coastal ocean with the

313　surf zone as a barrier, or not hinder shoreward migration (Shanks et al. 2010, Shanks et al.

314　2017a, Morgan et al. 2016, Morgan et al. 2017a). Most rocky shores are steep and, hence,

315　reflective, and hydrodynamics coupled with larval behavior tend to hinder the delivery of larvae,

316　including cyprids and mussels, to the shore. In contrast, more dissipative shores, including rock

317　platforms associated with wide dissipative surf zones, often contained bathymetric rip currents

318　that concentrate larvae in eddies (Fujimura et al. 2014, Morgan et al. 2016, Morgan et al. 2017b).

319　Barnacle larval settlement, recruits and population densities were significantly higher at more

320　dissipative than reflective surf zones (Shanks et al. 2017a).

321　　　　　Several studies used variations in recruitment at sites from central California (about 35 ºN

322　latitude) northward into Oregon to support the IUH (reviewed in Menge and Menge 2013). The

323　intensity of upwelling and its persistence decreased along this latitudinal transect; it was higher

324　in central and northern California and decreased northward with, the papers suggest, a sharp drop

325　occurring north of Cape Blanco, Oregon (Figure 1). Recruitment tended to be higher north of

326　Cape Blanco, consistent with the IUH. However, daily solar radiation (Shanks et al. 2017a) and

327　maximum intertidal temperatures as measured with Robomussels (Helmuth 1998, Helmuth et al.

328　2000, Helmuth 2016) also decreases along this latitudinal gradient of stations (Figure 1). In

329　addition, either due to chance or latitudinal variation in coastal geomorphology, many of the

330　stations surveyed north of Cape Blanco are rock platforms within wide more dissipative surf

331　zones (Figure 1), where settlement was high due to surfzone hydrodynamics (Shanks et al.

332　2017a). Lastly, runoff of nutrients from high precipitation may fuel phytoplankton production

333　that is several times greater in the waters over the Oregon and Washington continental shelf

334　(Hickey and Banas 2008), providing more food for adults and larvae thereby increasing

335　reproductive output or larval survival (Morgan 2001). Thus along this latitudinal transect of

336　stations, there are consistent trends in four variables all of which have the potential to increase

337　recruitment to the north.

338    At least two studies conducted along a longer latitudinal transect sampled sites with

339    enough variation in these variables that it might be possible to untangle their effects. 1) Broitman

340    et al. (2008) sampled mussel (*Mytilus*) and barnacle (*Balanus*) recruitment to Tuffy scrub pads

341    and Safety-Walk plates, respectively, at stations distributed from south of Pt. Conception and

342    within the Southern California Bight to northern Oregon. Note this study occurred before it was

343    discovered that Safety-Walk plates heat up rapidly in the sun (Shanks 2009) and that surfzone

344    hydrodynamics affect intertidal populations and the delivery of larvae to the shore (Rilov et al.

345    2008, Shanks et al. 2010). 2) Recently, Shanks et al. (2017a) surveyed the structure of barnacle

346    populations, density of adult *Balanus* and recruit density (individuals < 1.5 mm dia.) from San

347    Diego to northern Washington.

348    These studies sampled sites within the Southern California Bight where the

349    hydrodynamics are quite different from the coast to the north of Pt. Conception or seaward of the

350    Channel Islands. Within the Bight, flow along the coast is from the south, winds are weaker and

351    more variable, and upwelling is much weaker and less frequent, downwelling conditions are

352    more common (Checkley and Barth 2009). Along the coast northward from Pt. Conception,

353    upwelling-favorable winds during spring and summer increase in magnitude to around 38°N near

354    Bodega Bay and then decrease northward (Figure 1).

355    Along this latitudinal transect, solar energy (average daily solar radiation was obtained

356    from the National Solar Radiation Data Base; http://rredc.nrel.gov/solar/old_data/nsrdb/)

357    decreases monotonically from south to north (Figure 1), although the actual exposure of

358    intertidal organisms to solar energy is likely more complex depending in part on the timing of

359    daytime low tides (higher exposure occurs when low spring tides occur during the hottest time of

360    the day) (Helmuth et al. 2000). To capture this effect, we analyzed temperature data collected

361    using Robomussels (mussel models with an embedded thermistor) (Helmuth 2016) at a number

362    of study sites. Using these data, we calculated the average maximum low tide temperature

363    (Figure 1). To make this calculation, we first determined the average and standard deviation of

364    temperature over the entire time series at each site, added twice the standard deviation to the

365    average temperature, and calculated the average of all the temperatures higher than this

366    temperature, which we have defined as the average maximum low tide temperature.

367    We measured surfzone width as a proxy for surfzone hydrodynamics, wider surf zones

368    are more dissipative and narrow more reflective. Detailed description of the methods used to

369 measure surfzone width and reliability of the data are presented in Shanks et al. (2017a, c).

370 Briefly, we used images from Google Earth during spring and summer to determine the average

371 width of the surf zone immediately seaward of the sample sites. Width was from the most

372 seaward breaking wave to the swash line. The number of useable Google Earth images varied

373 from 3 to 14 and were taken between 2007 and 2014. The distribution of surfzone widths at the

374 study sites is likely a reflection of the distribution of coastal geomorphology (Figure 1). For

375 example, the geomorphology of the Big Sur coast (roughly Pt. Piedras Blancas, 35.7°N to Pt.

376 Lobos, 36.5°N) is very steep with few sandy beaches or more dissipative surf zones. North of

377 Cape Mendocino (40.35°N) dissipative surf zones are more common and a number of sites north

378 of Cape Blanco frequently sampled by intertidal ecologists are rock platforms associated with

379 wide more dissipative surf zones (e.g., Cape Meares, Yachats, Strawberry Hill, and Tokakee

380 Klootchan).

381 We reanalyzed data from Broitman et al. (2008) and Shanks et al. (2017a) to examine the

382 effect of solar radiation, average maximum low tide temperature, surfzone hydrodynamics as

383 indicated by surfzone width, and the strength of upwelling as indicated by alongshore wind stress

384 (see Shanks et al. 2017a for discussion of alongshore wind stress vs. the Bakon index as proxies

385 for upwelling) on recruitment of *Balanus* and mussels along the West Coast. Data for 1) average

386 solar radiation and surfzone width was available for each study site (see Shanks et al. 2017a, for

387 methods), 2) average alongshore wind stress during the spring and summer was calculated using

388 data from 15 NOAA weather buoys (see Shanks et al. 2017a for methods) and 3) Robomussel

389 temperature data are from 11 sites (Table 1). To assign values of alongshore wind stress and

390 average maximum low tide temperature to each study site from Broitman et al. (2008) and

391 Shanks et al. (2017a), we calculated regressions between latitude (independent variable) and the

392 physical variables of average maximum low tide temperature and alongshore wind stress

393 (dependent variables) and then used these regression equations to calculate the values of the

394 physical variables at each site (see Shanks et al. 2017a for methods) (Table 2). We calculated the

395 alongshore wind stress and average maximum low tide temperature for each of the three years of

396 data (2001-2003) that we analyzed from Broitman et al. (2008), calculated the average of these

397 values and used these averages in the regression analysis.

398 Broitman et al. (2008) surveyed the latitudinal and seasonal variation in *Mytilus* and

399 *Balanus* recruitment from 1997 through 2004, but all 26 sites were only sampled from 2001 to

400  2003. The following analysis is limited to these years. Data were presented as heat maps of the

401  log of the monthly recruitment rates (Broitman et al. 2008), so we estimated the recruitment rates

402  by comparing the heat map color scale to the color for the month with highest annual

403  recruitment.  We calculated linear regressions between the log of recruitment of *Mytilus* and

404  *Balanus* in the Broitman et al. and Shanks et al. data sets (dependent variables) and the averages

405  of daily solar radiation, maximum low tide temperature, alongshore wind stress, and log surfzone

406  width (independent variables).

407        In the Broitman et al. (2008) data, recruitment of *Mytilus* and *Balanus* were negatively

408  related to average daily solar radiation and average maximum low tide temperature with >60 to

409  almost 70% of the variation in recruitment explained by these variables (Figure 2).  Given the

410  heating of Safety-Walk plates when in the sun, the strong relationship between daily solar

411  radiation and average maximum low tide temperature and *Balanus* recruitment was expected.

412  What was not expected was that the recruitment of *Mytilus* to scrub pads responded similarly.

413  The open structure of scrub pads may not retain much moisture; perhaps exposing the mussel

414  recruits to desiccation stress. In contrast, the abundance of barnacle recruits (individuals <1.5

415  mm) surveyed on natural rock substrate by Shanks et al. (2017a) varied weakly with daily solar

416  radiation (~20% of the variation explained) and the average maximum low tide temperature

417  (12% of the variation explained). There were no significant regressions between alongshore wind

418  stress and any of the recruitment data (Figure 2). All three measures of recruitment, however,

419  varied significantly with surfzone width, although relationships to recruitment were weaker in

420  the Broitman et al. (2008) study (30 and 22% of the variation explained for mussels and

421  barnacles, respectively) than the Shanks et al. data on barnacle recruits (66% of the variation

422  explained). This difference might be related to the much stronger affects of daily solar radiation

423  and average maximum low tide temperature on recruitment to artificial substrates in the

424  Broitman et al. (2008) study than to the natural recruitment measured by Shanks et al. (2017a).

425        Broitman et al. (2008) found that the density of cyprid settlers on the recruitment plates

426  correlated with recruitment to the plates. Our reanalysis of their data found that recruitment

427  varied with surfzone width, hence, by logical extension, settlement likely also correlates with

428  surfzone width. This matches the findings by Shanks et al. (2017a); the density of recruits on

429  natural rock substrates and the weekly recruitment and daily settlement of barnacles to cleared

430  rock quadrates all varied with surfzone width, an indicator of surfzone hydrodynamics.

431      In an attempt to control for the effect of variation in coastal hydrodynamics (i.e.,

432  upwelling and downwelling) on barnacle recruitment and settlement, Shanks et al. (2017a)

433  surveyed closely spaced pairs of stations (several km to 100s of meters apart) with different

434  types of surf zones. At some station pairs, they also measured weekly recruitment and daily

435  settlement to natural rock surfaces. Surfzone widths at some of the pairs of stations were

436  similarly narrow while in other cases one station had a wide surf zone (more dissipative) and the

437  other narrow (more reflective). If barnacle larval settlement and recruitment depends on coastal

438  hydrodynamics (e.g., upwelling strength and persistence) then, given the close spacing of the

439  stations, these measures of barnacle recruitment and settlement should have been the same at

440  each station pair. If instead these measures vary with surfzone hydrodynamics, then these

441  measures should be similar at station pairs with narrow surf zones but different at station pairs

442  with wide and narrow surf zones (higher settlement and recruitment at the wide surf zone) and

443  this is exactly what was observed (Shanks et al. 2017a). This comparative experiment clearly

444  illustrated the importance of surfzone hydrodynamics on barnacle larval settlement and

445  recruitment in the intertidal zone.

446      In this reanalysis of recruitment data from Broitman et al. (2008) and Shanks et al.

447  (2017a), we found no support for an effect of upwelling strength as measured by alongshore

448  wind stress on recruitment, a strong effect of two measures of potential desiccation stress on

449  recruitment to artificial surfaces (Tuffy scrub pads and Safety-Walk plates), a weak effect of

450  potential desiccation stress on natural barnacle recruitment, a strong effect of surfzone

451  hydrodynamics as indicated by surfzone width on natural barnacle recruitment and a weaker

452  significant effect on recruitment to artificial surfaces. These results are not consistent with

453  Prediction 4, but are consistent with surfzone hydrodynamics regulating barnacle larval delivery

454  to the intertidal zone along the west coast of the USA.

455

456  **Prediction 5. Where offshore phytoplankton concentrations are higher due to currents or**

457  **upwelling, subsidies of phytoplankton to the intertidal zone will be higher.**

458      Resources from the coastal ocean subsidize communities and populations in the intertidal

459  zone (Polis et al. 1997, Krenz et al. 2011). The waters of the coastal ocean are sources of food

460  (plankton and detritus) and settling larvae that can sustain populations. Temporal and especially

461  spatial variation in these bottom-up subsidies have profound effects on the form and function of

462 intertidal populations (Menge 2000). Researchers have attributed variations in subsidies to the

463 shore to alongshore variations in the hydrodynamics over the continental shelf (Bustamante et al.

464 1995, Menge et al. 1999, Connolly et al. 2001, Menge et al. 2003, Broitman et al. 2008, Menge

465 and Menge 2013). Where phytoplankton populations are larger due to the hydrodynamics of

466 offshore waters, subsidies to the intertidal zone are hypothesized to be higher (Menge and Menge

467 2013). When or where phytoplankton subsidies are higher, the growth rate of filter-feeding

468 foundation species are higher and their reproductive output is larger (Leslie et al. 2005, Bracken

469 et al. 2012).

470        Above, we have discussed subsidies of larvae to the shore and related variation in these

471 subsidies to alongshore variation in surfzone hydrodynamics. Subsidies of phytoplankton to the

472 shore may also vary with surfzone hydrodynamics. In two month-long intensive studies of a

473 reflective and more dissipative surf zone around the Monterey Peninsula, California,

474 concentrations of coastal phytoplankton in the surf zone (subsidies) at a reflective shore were

475 generally 10 times lower than in the waters just seaward of the surf zone, whereas at a more

476 dissipative surf zone the reverse was true (Shanks et al. 2016, Shanks et al. 2017b).

477        To experimentally test if phytoplankton subsidies to the intertidal zone are set by

478 surfzone hydrodynamics, we attempted to control for phytoplankton concentrations in the coastal

479 ocean (Shanks et al. 2017c) by comparing closely spaced stations (median separation 1 km,

480 minimum 30 m) around Cape Arago, Oregon where surfzone width varied from a few meters to

481 more than 200 m (i.e., reflective to more dissipative surf zones). Station spacing was close

482 enough that the concentration of phytoplankton in the coastal waters was likely quite similar (see

483 Shanks et al. 2017c for a discussion of this assumption). Hence, if subsidies were set by

484 concentrations on the inner shelf, then concentrations at the study sites should have been similar,

485 but if they were set by surfzone hydrodynamics, the concentrations should vary with surfzone

486 width. We found that 65 to 90% of the variation in the concentration of coastal phytoplankton

487 taxa (*Pseudo-nitzschia*, *Chaetoceros*, and dinoflagellates) in the surf zone was explained by

488 surfzone width.

489        We reanalyzed data from Bracken et al. (2012), who sampled the concentration of

490 Chlorophyll *a* (Chl *a*) in surf zones adjacent to rocky shores in Oregon. We found that >85% of

491 the variation in Chl *a* concentration was explained by surfzone width (Shanks et al. 2017c). In

492 addition, Bracken et al. (2012) found that mussel growth varied directly with Chl *a*

493    concentration; hence, mussel growth must also have varied with surfzone width.  C. Salant

494    (Unpublished Data) measured reproductive output of mussels and barnacles at the same sites

495    sampled by Shanks et al. (2017c), and found that reproductive output varied with phytoplankton

496    subsidies, which in turn varied with surfzone width, as in Shanks et al. (2017c). She also found

497    that the concentration of coastal phytoplankton species in reflective surf zones was significantly

498    lower than seaward on the inner shelf and the reverse was true at more dissipative surf zones, as

499    did Shanks et al. (2016, 2017b).

500    Harmful algal bloom taxa (HABs) are coastal phytoplankton, and their concentration at

501    the shore varies with surfzone hydrodynamics (Shanks et al. 2016). Most exposure of humans to

502    HAB toxins occurs when people consume shellfish, mostly intertidal shellfish, which have

503    consumed HAB species. Thus, the contamination of shellfish by HABs likely varies with

504    surfzone hydrodynamics (Shanks et al. 2016).

505    At least over fairly short geographic distances (e.g., Monterey Peninsula, central Oregon,

506    and Cape Arago), surfzone phytoplankton concentrations have varied directly with surfzone

507    hydrodynamics: phytoplankton subsidies were much lower at more reflective than dissipative

508    surf zones irrespective of the concentration in the coastal ocean. Perhaps when tested over longer

509    distances where concentrations of phytoplankton in the coastal ocean are indeed different, while

510    controlling for surfzone hydrodynamics, the effect of coastal phytoplankton concentrations on

511    subsidies to the intertidal zone will become apparent. To more rigorously test the effect of

512    surfzone hydrodynamics on the concentration of phytoplankton in surf zones, sampling still

513    needs to be conducted both within surf zones of different types and seaward in the coastal ocean

514    along a gradient of offshore phytoplankton concentration.

515    Perhaps the closest dataset to this ideal is that presented in Menge and Menge (2013).

516    There are no measurements of offshore phytoplankton concentration, but the stations sampled

517    extend from northern California to northern Oregon and include stations from either side of the

518    South Island of New Zealand. These sites cover a range of upwelling conditions from sites with

519    weak upwelling to downwelling (New Zealand stations), strong persistent upwelling (California

520    stations) and intermittent upwelling (Oregon stations). To test for the effect of surfzone

521    hydrodynamics on phytoplankton subsidies, we digitized data in Figure 4 from Menge and

522    Menge (2013) using ImageJ and determined average surfzone widths from Google Earth images

523    of the study sites (See Shanks et al. 2017a, c for methods).

524         Menge and Menge (2013) found that surfzone concentrations of Chl *a* were related to

525 both the Bakun upwelling index and an index they created that measures the intermittency of

526 upwelling, the Intermittency index. The relationships were complex with lower Chl *a*

527 concentrations at low and high values of both the Bakun upwelling and Intermittency Indices

528 (Figure 3A,B redrawn from Menge and Menge (2013)). At stations in central Oregon with

529 similar or identical values of the Bakun upwelling and Intermittency Indices, however, the Chl *a*

530 concentration varied by a factor of 5 from 5 to 25 µg/L (Figure 3). This pattern of Chl *a*

531 concentration might be due to the chance distribution of wide and narrow surf zones among the

532 study sites. In Figure 3C and D, we plotted surfzone width with the Bakun upwelling and

533 Intermittency Indices; at low and high values of the indices, surf zones coincidentally tended to

534 be narrow while at intermediate values of the indices surfzone width ranged from narrow to quite

535 wide (> 150 m). When the surfzone Chl *a* concentration (dependent variable) was regressed with

536 surfzone width (independent variable), almost 65% of the variability in Chl *a* was explained by

537 surfzone width (Figure 4A); narrow more reflective surf zones contained lower concentrations of

538 Chl *a* than wider more dissipative surf zones.

539         Perhaps the effect of offshore coastal hydrodynamics would become apparent if we

540 scaled Chl *a* concentrations by the effect of surfzone hydrodynamics. We calculated the residuals

541 from the regression between surfzone width (independent variable) and Chl *a* concentration

542 (dependent variable) and then calculated regressions between these residuals (dependent

543 variable) and the Bakun upwelling index and the Intermittency index (independent variables);

544 these regressions were not significant (Figure 4 B, C). Thus, Prediction 5 is not supported, and

545 instead, as with subsidies of larvae to the shore, phytoplankton subsidies to the shore vary with

546 surfzone hydrodynamics.

547 **Conclusion**

548         Our reconsideration of the evidence for the IUH finds that the hypothesis is not

549 supported. 1) Larvae of many intertidal taxa are not found in the surface Ekman layer where

550 larvae would have to occur if upwelling were to transport them offshore and 2) larvae of

551 intertidal invertebrate species do not occur farther offshore during upwelling and closer to shore

552 during downwelling as proposed. 3) Daily settlement of barnacle cyprids and the abundance of

553 crab megalopae at the shore are not higher during downwelling and lower during upwelling, but,

554 instead vary with a fortnightly periodicity likely due to onshore transport by tidally generated

555  internal waves. 4) Recruitment of mussels and barnacles to artificial settlement substrates varied

556  inversely with two measures of desiccation potential, did not vary with the strength of upwelling

557  and downwelling, but did vary directly with surfzone width, an indicator of surfzone

558  hydrodynamics; larval subsidies were significantly higher where surf zones were more

559  dissipative. 5) Like larval subsidies, phytoplankton subsidies to the shore varied with surfzone

560  hydrodynamics. Shelf hydrodynamics clearly affect phytoplankton abundance, but in the data

561  currently available, this variation in abundance is overshadowed by the effect of surfzone

562  hydrodynamics on the delivery of subsidies to the shore. The IUH has persisted for three decades

563  even though critical tests of transport processes were not, until fairly recently, conducted at sea,

564  alternative hypotheses were not seriously evaluated including studies indicating that behavior is

565  effective at regulating cross-shelf transport of larvae (Shanks 1995, Queiroga and Blanton 2004,

566  Morgan 2014, Morgan et al. 2017b) and other zooplankton (Peterson et al. 1979, Peterson 1998).

567  To test the IUH, we have focused on the CCLME where the preponderance of studies

568  have been conducted, the hypothesis was originated by researchers on the West Coast and the

569  authors of this paper conduct their research there. Given that the hydrodynamics of wind-driven

570  coastal upwelling/downwelling is essentially the same at each of the eastern boundary current

571  systems, we suspect that what is true for the CCLME likely applies to these other systems as

572  well, although this assumption needs testing. Of particular interest is what happens in systems,

573  such as those off South Africa and Peru/Chile where the oxygen minimum layer is frequently

574  present below the mixed layer across the continental shelf; does this layer of low oxygen water

575  prevent larvae from swimming downward to avoid the surface Ekman layer? If larvae are unable

576  to avoid the surface Ekman layer, then they may, as predicted by the IUH, be transported

577  seaward during upwelling events.

578  The effect of surfzone hydrodynamics on the delivery of subsidies (phytoplankton and

579  larvae) to the shore should be similar everywhere. The effects are primarily due to the physics of

580  surf zones and physical processes are conservative. Researchers influenced by the IUH have

581  viewed alongshore changes in intertidal community structure as gradients or clines driven by the

582  gradual changes in the strength and persistence of upwelling along a coast. In our work on the

583  effects of surfzone hydrodynamics on subsidies to the shore, we have not seen gradients and

584  instead find the variation in the structure of intertidal communities along a coastline to be a

585  mosaic driven apparently largely by the form of the surf zone adjacent to the shore. The form

586    that a surf zone takes, dissipative to reflective, is largely driven by the slope of the bottom

587    beneath the surf zone. Coastal geomorphology can be consistent over long distances. For

588    example, the entire Big Sur coast of California is steep and nearly all of the surf zones at beaches

589    and rocky shores are narrow and more reflective. In other areas, the geomorphology can change

590    over short distances. This appears to be the case from roughly Cape Mendocino, California

591    through Oregon. Here we have found rocky shorelines with reflective surf zones adjacent to rock

592    platforms imbedded in more dissipative surf zones (e.g., Strawberry Hill vs. Boilers Bay). In

593    these situations, over surprisingly short distances (10s of m), we have seen order of magnitude

594    changes in the delivery of subsidies (larval settlers and phytoplankton food) to the shore (Shanks

595    et al. 2017a, Shanks et al. 2017c). What our studies suggest is that shores with more dissipative

596    surf zones and higher subsidies tend to have intertidal communities dominated by filter feeders

597    (particularly barnacles) while shores with more reflective surf zones tend to have communities

598    with far fewer filter feeders and denser populations of benthic macrophytes (Shanks et al. 2010,

599    E. Conser Unpublished Data). Our research on surf zones has forced us to see the world of

600    intertidal ecology from a very different perspective, one where benthic pelagic coupling and

601    intertidal community structure is largely controlled by very nearshore hydrodynamics, which in

602    turn is controlled by geomorphology.

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608

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822 Table 1.  Average maximum low tide temperature as measured by Robomussels at stations

823 sampled by Helmuth et al. (2016) along the west coast of North America. See text for the

824 methods.

825

| Station Name | Latitude, N | Longitude, W | Ave Max Low Tide Temperature, ºC |
|---|---|---|---|
|  |  |  |  |

| Coal Oil Point | 34.4067 | 119.8783 | 36.2 |
|---|---|---|---|
| Jalama | 34.4952 | 120.4969 | 33.7 |
| Piedras | 35.6658 | 121.2867 | 41.7 |
| Hopkins | 36.6219 | 121.9053 | 41.4 |
| Bodega Reserve | 38.3185 | 123.0740 | 42 |
| Cape Mendocino | 40.348 | 124.3650 | 33.3 |
| Trinidad | 41.0621 | 124.1493 | 31.7 |
| Cape Arago | 43.3066 | 124.4024 | 36 |
| Strawberry | 44.2499 | 124.1136 | 37 |
| Boilers Bay | 44.8306 | 124.0601 | 31.6 |
| Landing Beach | 48.3938 | 124.7355 | 28.3 |

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830 Table 2. Regression equations used to calculate alongshore wind stress and average maximum

831 low tide temperature at stations sampled in Broitman et al. (2008) and Shanks et al. (2017a).

| Regression | n | $R^2$ | P | Regression Equation |
|---|---|---|---|---|
| Alongshore Wind Stress, Broitman et al. (2008) analysis | 11 | 0.848 | <0.0004 | $y = 0.003028\,x^3 + (-0.3857\,x^2)+(16.217\,x)-224.479$ |
| Alongshore Wind Stress, Shanks et al. (2017a) analysis | 15 | 0.634 | <0.00006 | $y = 0.00224\,x^3 + (-0.2865\,x^2)+(12.0948\,x)-168.1436$ |
| Ave. Maximum Low Tide Temperature | 11 | 0.362 | =0.05 | $Y = -0.587\,x + 59.83$ |

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835     **Figure Captions**

836     Figure 1. Regressions of three environmental variables at study sites along the west coast of the

837     USA. Samples stations are those from Broitman et al. (2008) (open circles) and Shanks et al.

838     (Shanks et al. 2017a) (filled triangles). A) Alongshore wind stress during three years of the data

839     (2001-2003) from Broitman et al. (2008) reanalyzed here and from the study by Shanks et al.

840     (2017a). The dotted and dashed lines are the results of regressions (see Table 2 for regression

841     equations) between the alongshore wind stress data and latitude for the Broitman et al. and

842     Shanks et al. data, respectively. Wind stress values are from wind data collected by NOAA

843     weather buoys. B) Average daily solar radiation ($KWh/m^2/day$) at each station sampled by

844     Broitman et al. and Shanks et al. with the results of a regression between latitude and solar

845     radiation (dotted line). Open diamonds are the average maximum low tide Robomussel

846     temperatures (°C, see text for methods) with the results of a regression between latitude and the

847     average maximum low tide Robomussel temperatures (dashed line, see Table 2 for regression

848     equation). C) Average surfzone width as determined from Google Earth images. Note the

849     increase in the frequency of stations with wide ($\geq 100$ m) more dissipative surf zones north of

850     Cape Mendocino. The dotted and dashed lines are the results of regressions between surfzone

851     width and latitude for the Broitman et al. and Shanks et al. data, respectively. A description of

852     the techniques used to measure surfzone width and the reliability of the data are presented in

853     Shanks et al. (2017a) and Shanks et al. (2017c).  The vertical dotted lines indicate the locations

854     of prominent capes (PC, Point Conception; CM, Cape Mendocino; CB, Cape Blanco.)

855

856     Figure 2. Variation in the density of *Mytilus* and *Balanus* recruits ((A, D, G, J and B, E, H, K,

857     respectively, data from Broitman, 2008) and barnacle recruits (C, F, I, and L, data from Shanks

858     et al. 2017a) with four physical variables from the west coast of the USA. A-C) Average daily

859     solar radiation (($KWh/m^2/day$). D-F) Average maximum low tide temperature from Robomussels

860     (see text for details). G-I) Average alongshore wind stress in dynes. Positive (negative) values

861     are upwelling (downwelling) favorable. J-L) Surfzone width as determined from Google Earth

862     images (see Shanks et al. 2017a, c for methods). Note that if a Bonferroni correction was applied

863     to the set of four regressions calculated for each data set then the regression in F would not be

864     significant (corrected alpha = 0.0125).

865

866    Figure 3. Variation in Chl *a* concentration and surfzone width relative to two upwelling indices,

867    (A) the Bakun Upwelling index and (B) the Intermittency index (redrawn from Menge and

868    Menge (2013)). The dotted lines are the results of a regression analysis. See Menge and Menge

869    (2013) for a description of methods and statistical analysis. The Bakun Upwelling index is a

870    measure of the strength of upwelling while the Intermittency index was developed by Menge and

871    Menge (2003) as a measure of the frequency of upwelling. Triangles are data from the South

872    Island of New Zealand, diamonds are from Oregon stations, and circles from northern California

873    stations. In C and D, the Bakun Upwelling and Intermittency indices, respectively, are plotted

874    with average surfzone width at the sampled stations as determined from Google Earth images

875    (see Shanks et al. 2017a, c for methods).

876

877    Figure 4. Variation in Chl *a* concentration (data from Menge and Menge 2013) relative to three

878    environmental variables. A) Average surfzone width as determined from Google Earth images of

879    the stations sampled by Menge and Menge (2013). See Shanks et al. (2017a, c) for methods of

880    determining surfzone width from Google Earth images. Using the regression equation from (A),

881    we calculated residuals and then regressed these (dependent variable) against (B) the Bakun

882    Upwelling index and (C) the Intermittency index (independent variable, data from Menge and

883    Menge 2013). Neither regression was significant.
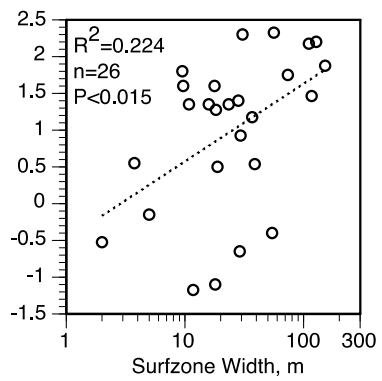
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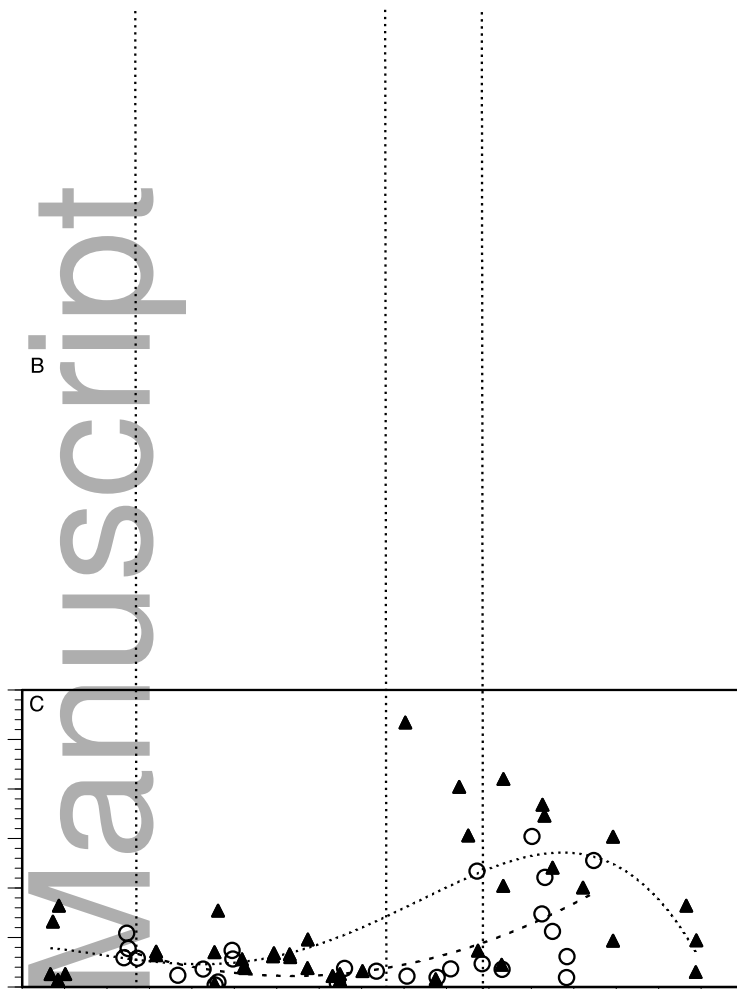


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888    Figure 1
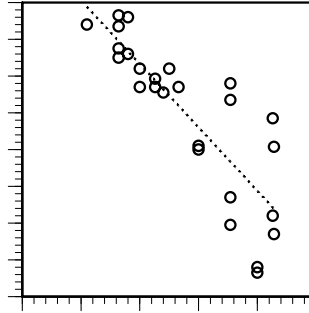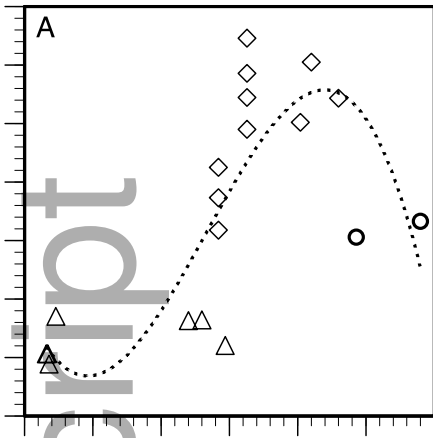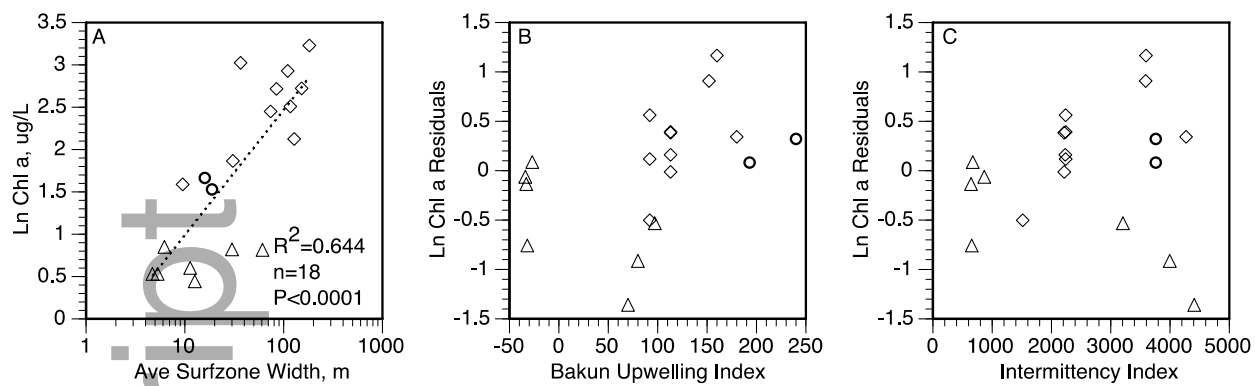
$R^2=0.119$
n=39
P<0.0315



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890

891 Figure 2

A

B

C

D

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Intermittency Index

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894    Figure 3

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899    Figure 4