

1 Non-native species colonization of highly diverse, wave swept outer coast habitats in
2 Central California

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16

17 **Abstract**

18 More non-native species (NNS) are reported from harbors, estuaries and protected
19 embayments than in wave-exposed, open coast habitats. In California (USA), hundreds of
20 NNS have become established in international ports, and dozens are known from smaller
21 estuaries. In contrast, only 22 NNS are reported from the state's 1350 km of open coast.
22 As a result, the perception that open coast habitats are not vulnerable to invasions has
23 persisted. Management and monitoring focuses on ports and estuaries; the last major
24 monitoring effort on the open coast occurred in 2004. Much of the species-rich Central
25 California coast is now part of a network of marine protected areas (MPAs). We surveyed
26 12 wave-swept rocky intertidal and eight subtidal sites (from 37°53'40 N 122°42'30 W to
27 36°31'16 N 121°56'22 W) for NNS. At least one NNS was detected at half of the sites
28 surveyed, but most were not widespread or abundant. One exception, a bryozoan in the
29 *Watersipora* spp. complex, known primarily from ports and estuaries, was found at
30 multiple sites, and was abundant at some. Another non-native, the alga *Caulacanthus*
31 *ustulatus*, was abundant at a single site. MPAs were just as likely as sites outside of

32 MPAs to have NNS. For subtidal sites, proximity to a harbor was correlated with the
33 abundance of non-natives. Our findings suggest that our study area is still relatively
34 uninvaded, but the success of *Watersipora* within some of these highly diverse rocky
35 shore sites underscores the potential vulnerability of high-value open coast systems to
36 invasions.

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38

39 **Introduction**

40

41 Hundreds of non-native species (NNS) are now established in the world's oceans
42 (Carlton 1999; Carlton and Ruiz 2005; Levin and Crooks 2011). As on land, NNS in the
43 ocean have negatively impacted ecological communities through predation, competition,
44 parasitism and habitat modification (Ruiz et al. 1997; Carlton 1999; Kappel 2005;
45 Williams and Smith 2007; Maggi et al. 2015). NNS also affect fisheries and aquaculture
46 (Kuris and Culver 1999; Leppäkoski et al. 2009; Vila et al. 2010; Galil 2011; Levin and
47 Crooks 2011), add to biofouling problems on vessels and maritime structures (Ruiz et al.
48 2000; Ruiz and Carlton 2003; Lewis and Coutts 2010), and interfere with marine
49 conservation and restoration efforts (Trimble et al. 2009; Albins and Hixon 2013). The
50 impacts of NNS interact with and may exacerbate other stressors in the marine
51 environment such as overfishing, chemical pollution, nearshore development, and climate
52 change (Keller et al. 2009; Claudet and Fraschetti 2010; Cebrian et al. 2012; Albins and
53 Hixon 2013; Sanford et al. 2014; Yuan et al. 2016).

54 As a broad pattern, more marine NNS are reported from harbors, estuaries and
55 wave-protected embayments (hereafter bays) than from the open coast (Carlton 1979;
56 Ruiz et al. 1997; Wasson et al. 2005; Preisler et al. 2009; Ruiz et al. 2009; Bumbeer and
57 Moreira da Rocha 2016; Simkanin et al. 2017). One simple explanation of this pattern is
58 greater supply: typically there are more potential invasion vectors such as shipping and
59 aquaculture in bays than along the open coast (Hedgpeth 1968; Carlton 1979). These
60 areas may also retain larvae and other propagules released by colonizing organisms,
61 which may contribute to greater success in establishment (Preisler et al. 2009), although
62 the relationship between larval supply and invasion success is not straightforward
63 (Simkanin et al. 2017). Another possible explanation is that the characteristics typical of
64 NNS limit their distribution: they tend to be calm-water organisms and therefore pre-
65 adapted to living in recipient bays (Carlton 1979; Ruiz et al. 1997). Given their presence
66 in harbors and human-modified areas from source regions around the world, they may
67 also be pre-adapted to disturbed habitats and novel environments (Carlton 1979; Bulleri
68 and Airoidi 2005; Glasby et al. 2007). Additionally, differences in ecological processes

69 between bay and outer coast habitats may play an important role. Open coast habitats
70 tend to be more species-rich than bays, and higher native-species diversity may result in
71 higher biotic resistance through increased competition or predation (Elton 1958; Carlton
72 1979; Stachowicz et al. 2002; Wasson et al. 2005; Shinen et al. 2009; Veiga et al. 2014),
73 although evidence for this is equivocal (Williams and Smith 2007; Jeschke et al. 2012;
74 Hackerott et al. 2013). Of course, these mechanisms are not mutually exclusive; it is
75 likely that some combination of invasion opportunity, species traits, habitat
76 characteristics and history, and ecological processes are responsible for the pattern of
77 fewer invasions on open coasts (Farrell and Fletcher 2006; Ruesink 2007).

78 However, open coast systems are certainly not immune from invasions. From a
79 global perspective, there are many examples of NNS that have become established
80 outside of bays, in some cases with significant ecological and economic impacts. For
81 example, in rocky intertidal systems, established NNS include the crabs *Hemigrapsus*
82 *sanguineus* and *Carcinus maenas* on the US Atlantic coast (Steneck and Carlton 2001),
83 the oyster *Crassostrea gigas* on west coast of Canada (Ruesink 2007), the mussel *Mytilus*
84 *galloprovincialis* in South Africa (Griffiths et al. 1992), and the solitary tunicate *Pyura*
85 *praeputialis* in Chile (Caro et al. 2011). The lawn-like green alga *Caulerpa taxifolia* is
86 now widespread in the Mediterranean Sea from the shallow subtidal to depths of 100 m
87 (Aplikioti et al. 2015), and the kelp *Undaria pinnatifida* has established in New Zealand
88 kelp forests (Russell et al. 2008). The corals *Tubastraea tagusensis* and *T. coccinea* are
89 spreading through reefs in the tropical Atlantic (Fenner and Banks 2004; Lages et al.
90 2011) and the lionfish *Pterois volitans* is having devastating impacts in the Caribbean and
91 tropical Atlantic (Albins and Hixon 2008).

92 Despite these examples, the idea persists that invasive species are not a major
93 concern for open coast ecosystems, particularly where these systems are diverse and less
94 disturbed by human activities (Steneck et al. 2002; Foss 2008; Edelist et al. 2012; Office
95 of National Marine Sanctuaries 2015). In California (USA), while NNS are
96 acknowledged by state and federal agencies as a potential threat to marine resources, the
97 state's marine protected areas (MPAs) focus their primary management efforts on
98 monitoring and protection of key native species, including associated fisheries (California
99 Department of Fish and Wildlife 2015). In a recent report ranking relative threats within

100 the Monterey Bay National Marine Sanctuary, NNS were listed as an important stressor
101 for estuarine locations, but not for nearshore or seamount environments within the
102 sanctuary (Office of National Marine Sanctuaries 2015). To date, surveys targeting NNS
103 on the coast have been infrequent (see Maloney et al. 2006; Foss 2008), and post-
104 invasion management activities are rare (authors' personal obs., but see Culver and Kuris
105 2000).

106 The lack of management focus on invasions on the open coast is unsurprising
107 given the distribution of NNS, which are mostly found in the state's bays and estuaries.
108 San Francisco Bay is an extreme example, with more than 250 established NNS (out of
109 the state's 290), but even smaller bays like Humboldt Bay, Tomales Bay and Elkhorn
110 Slough each have more than 60 such species (Ruiz et al. 2011). In contrast, open coast
111 habitats along the state's 1350 km coastline appear to have been relatively free of
112 invasions (Carlton 1979; Hedgpeth 1968; Cohen and Carlton 1995; Wasson et al. 2005;
113 Maloney et al. 2006; Zabin et al. 2013), with only 22 NNS previously reported from
114 outside of bays (Ruiz et al. 2011).

115 Thus, we were surprised when, during a citizen-science "bioblitz" (a one-day
116 event in which participants attempted to find and identify as many species as possible at
117 several study sites) in May 2014 we discovered numerous colonies of a non-native
118 bryozoan genus, *Watersipora*, at a rocky, wave swept intertidal site on the open coast in
119 the Marin Headlands, north of San Francisco Bay. A species of *Watersipora* has been
120 reported from California since 1963 (Cohen and Carlton 1995), as *Watersipora*
121 *subtorquata*, which is likely a species complex (Vieira et al. 2014, see Discussion). It is
122 now present in all major bays in the state (Fofonoff et al. 2017), with only a single report
123 from natural substrate on the open coast rocky intertidal (in Southern California, Pister
124 2009). The discovery of *Watersipora* in the Headlands, coupled with increasing reports of
125 NNS on natural substrate in wave-exposed environments in Southern California over the
126 past several years (Pister 2009; Miller et al. 2011; Kaplanis et al. 2016; see Simons et al.
127 2016 for reports from artificial substrates), suggested to us that a survey for NNS on the
128 outer coast in our region (Central California) was warranted. Northern range expansions
129 of warm-water adapted native species have been increasingly reported on the California
130 coast (Barry et al. 1995; Schultz et al. 2011; Cavole et al. 2016), and it might be expected

131 that NNS established on the outer coast in the southern portion of the state could
132 similarly be expanding north. While several past and ongoing biological surveys have
133 noted the presence of non-native species on the outer coast in this region (Zabin et al.
134 2013; R. Gaddam perscomm. 2015), it had been nearly 10 years since the previous
135 focused study (Maloney et al. 2006; Foss 2008), and very little quantitative data on these
136 species are available.

137 Our study's main objectives were to: 1) provide a broad scale characterization of
138 the distribution of NNS in the rocky intertidal through the collection of baseline data
139 along Central California's open coast, and 2) at a finer scale, record the presence and
140 abundance of NNS in intertidal and subtidal locations at increasing distances from a
141 coastal harbor within our larger study area. Both measures test for possible spill over of
142 NNS from bays to exposed outer coast habitat, providing a case study of invasions in an
143 area renown for its native species diversity.

144

145 **Material and Methods**

146 *Study location*

147 Our broad study area encompasses ~275 km along the Central California coastline
148 (Figure 1). This area is included within the Greater Farallones National Marine Sanctuary
149 north of San Francisco and the Monterey Bay National Marine Sanctuary south of San
150 Francisco Bay. Many of these study sites also fall within the state network of marine
151 protected areas (MPAs, see Table 1).

152 The Central California region, known for its high diversity of native marine
153 species (Abbott and Hollenberg 1976; Carlton 2007; Zabin et al. 2013) also includes a
154 major international port, San Francisco Bay, which is highly invaded, and several smaller
155 coastal harbors and estuaries from which NNS have also been reported, serving as
156 potential source populations for spread of NNS to the adjacent outer coast (Cohen and
157 Carlton 1995; Wasson et al 2001; Ruiz et al. 2011; Zabin et al. 2014).

158 The nearshore habitats within Monterey Bay National Marine Sanctuary, and
159 particularly within the Monterey area where we conducted our finer scale survey, are
160 species rich and diverse, and include productive kelp forests, one of North America's
161 largest underwater canyons, and extensive rocky shores. The area is home to one of the

162 most diverse marine ecosystems in the world, including 37 species of marine mammals,
163 over 180 species of sea and shore birds, 500 species of fishes, and numerous invertebrates
164 and algae (Office of National Marine Sanctuaries, 2015).

165

166 *Study sites*

167 We surveyed 12 rocky intertidal sites in fall 2014 and spring-summer 2015, and
168 eight subtidal rocky reef sites in fall 2014 (Fig. 1). In addition to our own surveys, we
169 report other unpublished species occurrence data collected within our study area.

170 We took several factors into account in selecting sites. First, we wanted an
171 intertidal sampling effort along as broad a study area as possible given logistical
172 constraints. Secondly, we were interested in sampling areas that are relatively close (<20
173 km) to potential sources of NNS (harbors and estuaries), and we wanted to include sites
174 with high natural resource value (as designated by their inclusion within MPAs) as well
175 as sites not designated as MPAs. Sites were located near San Francisco Bay and harbors
176 at Pillar Point, Santa Cruz, and Monterey (harbors and estuary names in boxes, Fig. 1).
177 Finally, we also included locations where NNS on our target list (see below) had been
178 reported, but where quantitative data had not been collected. Intertidal sites were
179 surveyed at least once during low tides in December 2014 and May and June 2015 (Table
180 1). Surveys were made a second time at the three sites with the highest abundances of
181 non-natives, and we returned to one of these (Soquel Point) in June 2016 to assess
182 possible spread of a species we noted there in 2014 and 2015.

183 For our finer-scale study, in October-November 2014, we focused on sites on or
184 immediately south of the Monterey Peninsula, hereafter “Monterey area” (Inset, Fig. 1).
185 All of these study sites are within MPAs. In addition to the intertidal sites mentioned
186 above, we surveyed popular dive sites along a wave-exposure gradient and increasing
187 distance from a potential source of NNS -- the Monterey Harbor and private Breakwater
188 Marina (Table 2). Private yachts and a few commercial fishing vessels make up the bulk
189 of the vessel traffic at these two connected marinas, although larger oceangoing vessels
190 and cruise ships occasionally anchor adjacent to the marinas (Ashton et al. 2011). At least
191 25 NNS have been reported from these marinas, including several of our target taxa
192 (Ashton et al. 2011, Marraffini and Geller 2015), but had not been previously reported

193 west of the breakwater, a 400 m concrete and rip-rap barrier that protects both harbors.
194 For one of our target taxa (*Watersipora*) we also reviewed photographs from earlier dive
195 surveys in the region made by one author (SIL), as well as data collected over several
196 years at one site, Hopkins Marine Station, by student divers in a Kelp Forest Ecology
197 class taught by another author (JW).

198

199 *Target taxa*

200 On open coast rocky shores within our study region, there are hundreds of species
201 of native marine invertebrates and macroalgae (Carlton 2007; Abbott and Hollenborg
202 1976; Zabin et al. 2013). There are also hundreds of NNS in Californian waters, and
203 many are cryptic and difficult to identify (Fofonoff et al. 2017). Searching for all
204 possible NNS would have required an enormous effort, beyond the scope of this study. In
205 consultation with experts (see Acknowledgements) we developed a target list of taxa on
206 which to focus our survey efforts (Table 3). These included species that had been found
207 on the open coast in Southern California, which might be spreading north (Ruiz et al.
208 2011), and taxa that are highly abundant in fouling communities in Central California
209 bays that might be able to survive on the open coast. Some of these species, such as *W.*
210 “*subtorquata*,” (hereafter “*Watersipora*”) had been seen on the open coast, but little or
211 no quantitative data on abundance existed. We also attempted to mostly select NNS that
212 were conspicuous and morphologically distinct, so that the majority of the identifications
213 could be made *in situ*. Two of our taxa are actually species complexes, for which clear
214 morphological differences do not exist or are extremely difficult, *Bugula* “*neritina*” and
215 *Watersipora* (see Discussion). We did not attempt to identify these organisms to species
216 level, but samples were collected for later genetic analysis.

217

218 *Survey methods*

219 For both intertidal and subtidal surveys, we searched for target species within 30 x
220 2 m belt transects. A 30 m transect tape was placed on the substrate and researchers
221 looked for target species within 1 m on each side of the tape (total search area 60 m² per
222 transect), on both horizontal and vertical surfaces, in cracks and crevices, and under rocks
223 where applicable. To facilitate the search effort, a PVC quadrat (0.5 m per side) was used

224 to subdivide the belt transect into contiguous, non-overlapping cells, for a total of 240
225 such quadrats per transect. Intertidal transects ran parallel to shore. Subtidal transects
226 followed a compass bearing selected to maintain a constant depth profile on rocky
227 substrata, which was generally parallel to shore.

228 We placed intertidal transects at high, mid- and low-tide zones (1-2 transects per
229 elevation), as indicated by ecological communities typical of these elevations (Ricketts et
230 al. 1985). Constraints of tide, daylight, and shoreline slope limited our ability to use these
231 methods at every site (Table 1). In addition, we completed broad (i.e. site-level) surveys
232 by walking for ~20 minutes in areas not sampled with transects. At two sites, McAbee
233 Beach and Lovers Point, appropriate substrate was patchily distributed and thus
234 precluded transects; here we completed site-level searches only to record
235 presence/absence data. At subtidal sites, we surveyed two to three transects (Table 2),
236 depending on the size of the site, at depths from ~3 to ~8 m.

237 Within each quadrat, we made two types of abundance estimates: counts of
238 unitary organisms (such as individual thalli) and percent cover of modular organisms
239 (e.g., turf algae, bryozoan colonies, compound tunicates, and sponges)(Dethier et al.
240 1993). Percent cover was estimated visually using 5% bins, with the exception of
241 extremely low cover (only one or two very small patches), which we categorized as 1%
242 cover. In addition to counts and estimates of percent cover within a quadrat, we also
243 noted primary substrate type and orientation, and depth. If the target NNS was an
244 epibiont, we recorded the species on which it was growing. For subtidal surveys in
245 locations where target NNS were present in most quadrats and full surveys of the transect
246 were not possible due to logistical constraints, divers recorded only presence/absence
247 data within quadrats at 0.5 m intervals along the meter tape and the more detailed data
248 described above was collected for quadrats at each 1 m interval.

249 Between 2009-2012 and in 2015-2016, students at Hopkins Marine Station
250 collected data on abundance of *Watersipora* as part of a Kelp Forest Ecology class taught
251 by JW. Students recorded abundance of the bryozoan in a 40 x 40 m area, making visual
252 estimates of cover within 0.25 m² quadrats randomly placed within four quadrants at the
253 study area. Each diver within a buddy pair made his or her own estimate, and the average
254 of the two was used. To facilitate visual estimates, quadrats were subdivided into 25

255 squares, each representing 4% of the sample area. In 2010, students also began recording
256 substrate angle (horizontal, vertical or sloped) and other species present.

257

258 *Data analysis*

259 We present data at several levels. First, we report all target taxa found at each site,
260 which allows us to include taxa that were found outside of transects as part of the timed
261 searches. Second, for each site we report data from the transect surveys, including (a) the
262 number and percent of transects in which target taxa were found (of all transects at a site)
263 and (b) frequency of occurrence of target taxa *within* transects (of all quadrats within a
264 transect). We also generated percent cover estimates for each transect by averaging
265 across all quadrats within a transect. Visual cover estimates, while sometimes not as
266 precise as point counts, are reliable protocols to detect differences in studies such as ours
267 (see discussions in Dethier et al. 1993; Johns et al. 2015; Nguyen et al. 2015). These data
268 are presented cautiously here, as a way to compare relative differences in abundance
269 among taxa and locations. Most locations were surveyed one time only, and for intertidal
270 sites, we had just a single transect per tidal elevation. The data described above thus
271 represent initial baseline information, and the trends in the summary statistics generated
272 from these data were used for informal comparisons between sites.

273 We used a Fisher's exact test to determine whether there was a difference in the
274 number of target taxa detected in sites inside vs outside MPAs. Fisher's exact tests are
275 more appropriate than chi-square tests for datasets with small sample sizes. We used data
276 from our first visit to each site in this analysis to eliminate bias due to a larger sample
277 size at the sites surveyed more than once.

278 For the subtidal surveys in the Monterey area, we used a generalized linear model
279 (GLM) to test whether the occurrence of target taxa was correlated with distance from the
280 Monterey Harbor. GLMs are a useful approach for fitting models where the variance is
281 not normally distributed and/or constant. For each transect, we generated a frequency of
282 occurrence measure for target taxa (the number of quadrats in which target taxa were
283 found divided by the total quadrats per transect). We estimated the distance from the edge
284 of the harbor closest to our study sites to the midpoint of each site. We added a small
285 value (0.0001) to the frequency of occurrence measure for transects in which no target

286 taxa were found, and log transformed distance from harbor. For the GLM, we used a
287 gamma error distribution and log-link function. All analyses and graphs were performed
288 in R (version 3.1.2: R Core Team 2014), with the packages MASS, car, and ggplot.

289

290 **Results**

291 *Regional distribution and abundance of NNS*

292 We recorded five of our 16 target taxa – the bryozoans *Watersipora* and *Bugula*
293 “*neritina*”, the sponge *Hymeniacidon sinapium*, the red alga *Caulacanthus ustulatus*, and
294 the brown alga *Colpomenia peregrina* from intertidal transects at six of our 12 sites
295 (Table 4, Fig. 1). Breakwater Cove had three target taxa, Soquel Point had two, and all
296 other sites had only one. Target taxa were just as likely to be found within MPAs as at
297 sites outside of MPAs (Fisher’s exact test for count data, $P=1$, odds ratio 0.53, 95% CI:
298 0.026-8.29).

299 *Watersipora* was encountered at four sites, and *Hymeniacidon sinapium* at two
300 sites. The other three species were each found at a single site. With the exception of *C.*
301 *ustulatus*, taxa were found in the mid and low intertidal zones only (Table 4). *C.*
302 *peregrina* was found only in the summer. With a few exceptions, discussed below, target
303 taxa were relatively rarely encountered within transects and did not represent high levels
304 of cover (Figs. 2,3).

305

306 *Intertidal distribution and abundance*

307 Bryozoans

308 *Watersipora* was found at four intertidal sites (Table 4) and was particularly
309 abundant and broadly distributed at two of these: Slide Ranch and Breakwater Cove
310 (Figs. 2,3). At Slide Ranch, it was present in 45% (SE +/-2.5) of quadrats in the low zone
311 and 26% (SE +/-2) of quadrats in the mid (Table 4, Fig. 2). At Breakwater Cove,
312 *Watersipora* was present in 12%(+/-SE 5.4) of low intertidal quadrats and 1.5% (+/-0.5
313 SE) of mid-intertidal quadrats (Table 4, Fig. 2). In the single low intertidal transect we
314 surveyed at Muir Beach, it was found in 5% of low intertidal quadrats, and it was not
315 found at all in the mid-intertidal. Just two specimens were found at Hopkins Marine

316 Station in a single quadrat in one of the two mid-intertidal transects, and none in the low
317 zone.

318 Colonies of *Watersipora* were typically small in the intertidal zone, and
319 represented 1-10% cover in most quadrats where it was present, with occasional large
320 colonies comprising >20% cover (Figs. 3, 4a). The bryozoan was growing nearly
321 exclusively on vertically oriented surfaces (89% of all observations) or on horizontal
322 surfaces under rocks or under hangs (10% of all observations), mostly on natural rock,
323 but also attached to a wide variety of substrates, including rip-rap, fleshy red and brown
324 algae, upright and encrusting coralline algae and other bryozoans.

325 *Watersipora* was also found in the intertidal zone near Santa Maria Creek in
326 Drakes Bay, Pt. Reyes National Park (Fig. 1, K.A. Miller, perscomm 2014) in July 2014,
327 but abundance data were not collected.

328 *Bugula "neritina"* was found only at Breakwater Cove. We recorded it just 12
329 times across all transects and sample dates, always at low cover (<10%) within quadrats,
330 which resulted in it representing far less than 1% cover within transects (Figs. 2, 3). We
331 found it twice in mid-intertidal zone transects; the other sightings were in the low
332 intertidal, on vertically oriented surfaces, growing on natural rock and encrusting
333 bryozoans, including *Watersipora*.

334

335 Algae

336 We detected the red alga *Caulacanthus ustulatus* at only one site, Soquel Point.
337 The alga was present within a single transect at this site, a vertically oriented armored
338 cliff face. It was attached primarily to the native mussel *Mytilus californianus* (Fig. 4b),
339 but also to the substrate, and located below the zone of the native turf alga *Endocladia*
340 *muricata*. There it was found in 28.6% (SE +/-14%) of the quadrats surveyed between
341 2014 and 2015, although it represented less than 1% cover (Figs. 2, 3). On a subsequent
342 visit to the site in 2016, the alga was also found to be abundant on mussels, natural rocks
343 and rip-rap approximately 250 m west of our sampling site. In this new location, it was
344 growing over a stretch of shoreline ~150 m long, with some very dense patches (Fig. 4c).
345 We estimated cover on this shoreline in December 2016 at 19% (detailed data Online
346 Resource 2, transect name "Rockview"). We did not find *E. muricata* in this area.

347 *C. ustulatus* was also found in the intertidal zone near Santa Maria Creek, Drakes
348 Bay, Pt. Reyes National Park (Fig. 1, K.A. Miller, perscomm 2014) in July 2014.
349 Abundance data were not collected. This species has been previously reported from
350 Natural Bridges (PISCO/MARINE,
351 www.eeb.ucsc.edu/pacificrockyintertidal/sitepages/terracepoint-bio.html) but we did not
352 detect it during our surveys there. It had also been reported from the rocky intertidal at Pt.
353 Pinos in Pacific Grove, near our Coral Street site (PISCO/MARINE, unpublished data),
354 but no quantitative data were recorded.

355 The native and non-native species of *Colpomenia* are difficult to distinguish in the
356 field. *Colpomenia* species were found at three sites, Slide Ranch, Mavericks and
357 Breakwater Cove. All specimens collected at Breakwater Cove were identified as *C.*
358 *peregrina* (non-native); specimens from the other sites were all the native *C. bullosa*. At
359 Breakwater Cove, *Colpomenia* was more abundant in the low zone (11% of quadrats, +/-
360 SE 4), than in the mid (found in 4% of quadrats in a single transect), however it
361 represented less than 1% cover (mean 0.3% +/-0.2% SE) even in the low zone (Figs. 2,3).

362

363 Sponges

364 We found the sponge *Hymeniacidon sinapium* at two sites, Natural Bridges and
365 Soquel Point (Table 4). The sponge was discovered during timed searches at both sites in
366 2014, and in a single quadrat in 2015 at Soquel Point. At both sites, only a few specimens
367 were found, all of which were small (<5 cm²) and encrusting, attached to substrate or
368 other sponge species.

369 A sponge species not on our target list, *Plocamiancora igzo*, was collected from
370 the low intertidal at Hopkins Marine Station, and appears to be a range expansion from
371 Southern California (D. Elvin perscomm 2017).

372

373 *Subtidal distribution and abundance*

374 With the exception of a single specimen of *Colpomenia peregrina* found at
375 Breakwater Cove, *Watersipora* was the only target NNS found in our subtidal surveys
376 (Table 4). In these surveys, we found *Watersipora* at the four sites closest to the harbor:
377 Breakwater Cove, McAbee Beach, Hopkins Marine Station, and Lovers Point (Table 4,

378 Fig. 1 inset). We did not find the bryozoan at Coral Street, or at any of the four sites
379 farthest from the harbor.

380 Across the subtidal sites, *Watersipora* was more frequently encountered at sites
381 closest to the harbors (Fig. 5). This pattern of a decrease in *Watersipora* occurrence with
382 distance from Monterey Harbor was statistically significant (GLM, pseudo $r^2 = 0.875$,
383 $P < 0.0001$, $N = 23$). The bryozoan was most frequently detected at Breakwater Cove,
384 where it was found in 29% (SE $\pm 5.3\%$) of all quadrats (Fig. 6a). At McAbee Beach, it
385 was found in 9.5% (SE $\pm 3.5\%$) of quadrats (Fig. 6a). At Hopkins Marine Station, it was
386 found in 7.6% (SE $\pm 3.2\%$) of quadrats, and at Lovers Point in 1% (SE $\pm 0.6\%$) of
387 quadrats (Fig. 6a). Transect-level cover was low at all sites ($< 5\%$), however, higher
388 density quadrats were also encountered (Fig. 6b).

389 We mostly recorded *Watersipora* from natural rock (80% of observations across
390 all quadrats), but colonies were also attached to a wide variety of surfaces, including rip-
391 rap, metal reinforcing bar (rebar) and old metal pipes, fleshy and encrusting algae,
392 barnacles, crabs, tubeworms and other bryozoans. The bryozoan was more frequently
393 recorded on horizontal surfaces (75% of instances), but large foliose colonies tended to
394 be found only on vertical surfaces. Living organisms represented 7% of substrates on
395 which *Watersipora* was found, and included the decorator crab (*Loxorhynchus crispatus*).
396 *Watersipora* was also being used as substrate/habitat by other species. For example, at
397 Lovers Point, we observed many brittle star rays extending from large foliose colonies.

398 *Watersipora* had been photographed in earlier dive surveys in the area by SIL on
399 the Monterey Peninsula at Eric's Pinnacle in 2007 and at Ventura Rocks, south of Pt.
400 Lobos in Big Sur in 2008 (Fig. 1), but quantitative data were not collected. In the student
401 surveys at Hopkins Marine Station, mean percent cover of *Watersipora* within a 40 x 40
402 m study plot varied from a high of 4% (SE $\pm 1.8\%$, $N = 33$) in August 2009 to a low of
403 0.7% (SE $\pm 0.3\%$, $N = 32$) in August 2011. In 2009, *Watersipora* was found in 56% of
404 quadrats, in 2010 in 33% of quadrats, and in 25% of quadrats in 2011, 2012, 2015, and
405 2016. Students recorded colonies on horizontal faces of rocks about 50% of the time, and
406 25% of the time on vertical and sloping faces.

407

408 **Discussion**

409

410 *Distribution and abundance of NNS on the open coast*

411 Our study documented extensive distribution of the bryozoan *Watersipora* at
412 several rocky intertidal and kelp forest sites in Central California, including sites within
413 the state's MPA network. Although *Watersipora* has been reported from rocky intertidal
414 shores around the world, these have been primarily in calm-water environments (Gordon
415 1967; Morton and Miller 1968; Cohen et al. 2005; but see Malherbe and Samways 2014,
416 who report it from a semi-protected open coast). We know of one earlier finding of
417 *Watersipora* from natural substrate at a wave-exposed intertidal site (Pister 2009) and
418 from artificial substrates (oil rig platforms) in open-coast subtidal habitats in Southern
419 California (Simons et al. 2016; Page et al. 2006). Ours is the first report from the open-
420 coast intertidal in Central California and the first from natural substrates in a kelp forest
421 habitat. Given the bryozoan's long history of being found nearly exclusively in ports and
422 estuaries in California, we were struck by how widespread and abundant it now is on the
423 open coast within our study region. While the bryozoan's presence at Breakwater Cove
424 might have been predicted, given the proximity of this site to a harbor and its relative
425 protection from waves, the high abundance of *Watersipora* at Slide Ranch, an exposed,
426 remote site ~12 km from the mouth of San Francisco Bay, is particularly noteworthy.

427 The cause of this apparently recent spread to the outer coast is not clear. Possible
428 explanations include genetic changes resulting in adaptation to open-coast conditions, or
429 of the arrival of a new clade or cryptic species better adapted to such conditions.
430 Taxonomic confusion over the species or species complex known as *W. "subtorquata,"*
431 makes sorting out this latter idea difficult. Molecular surveys identified two clades of *W.*
432 "*subtorquata*": *W. subtorquata*, *W. arcuata*, and an undescribed *Watersipora* species
433 unknown in California waters (Mackie et al. 2012); however, the most recent
434 morphological revisions to the taxonomy of the *Watersipora* genus (Vieira et al. 2014),
435 identified only *W. subatra*, *W. atrofusca*, and *W. arcuata* from the state, though few
436 samples were examined from the region of our study. None of these are native species.
437 *Watersipora arcuata* can easily be distinguished from the other morphologies and is not
438 present in our outer coast samples. Morphologically, all of our outer coast specimens
439 appear to be the non-native *Watersipora subatra*, based on the presence of the lateral oral

440 septula, and the shape and size of the oral sinus (Vieira et al. 2014), but additional
441 collection needs to be done to confirm that all are this species. Further, we cannot
442 distinguish the species in earlier reports beyond that they are similar to *W. subtorquata*.
443 A study pairing both molecular and morphological techniques is needed to reconcile the
444 taxonomy of *Watersipora* on the California coast and shed light on whether the
445 *Watersipora* species at our sites represents a new introduction or the spread of an existing
446 invader from harbors and bays.

447 If the latter case is true, spread to the outer coast may have resulted from a change
448 in environmental conditions such as warmer waters or changes in current patterns, or
449 from continual inoculation from small boats or other locally operating vectors, such as
450 infected fishing or dive gear, which have been implicated elsewhere in other invasions
451 (Relini et al. 2000; Bullard et al. 2007; Williams and Smith 2007; Bacela-Spychalska et
452 al. 2013). It is also possible that colonization of the open coast is simply due to a gradual
453 build up of populations within bays, leading to a spillover into nearby coastal areas.
454 In addition to dispersal via larvae, large foliose colonies have been observed to survive
455 detachment from substrates; these can roll along the seafloor like tumbleweeds, possibly
456 dispersing living fragments and larvae some distance from their original attachment point
457 (Aiken 2014). Elsewhere viable colonies of this genus have also been observed on
458 floating seaweed, suggesting another potential dispersal mode (Kuhlenkamp and Kind
459 2013).

460 We also report the first quantitative data on abundance of the red turf alga,
461 *Caulacanthus ustulatus* from our study region. This alga had been previously seen at our
462 study sites at Soquel Point and Natural Bridges (K.A. Miller, R. Gaddam, perscomm
463 2014), but was not detected in earlier surveys from the late '90s (Zabin et al. 2013).
464 While abundance was still low in our study transect when we revisited this site in June
465 2016, we found a much larger, denser patch slightly west of our transect location. Both of
466 these patches appear to be relatively new; they were not seen in a survey at this site in
467 2011 (JSP, unpubl data.). At Southern California sites where it is abundant (40-70%
468 cover) on the open coast, *C. ustulatus* has had demonstrable impacts on the composition
469 of macroalgae and invertebrates in the upper intertidal zone (Smith et al. 2014). Our most

470 recent survey suggests that *C. ustulatus* is likely spreading just west of our study location.
471 This discovery warrants further survey efforts.

472 In contrast to the extensive distribution of *Watersipora*, the other NNS we found
473 were neither widely dispersed nor (with the exception of *C. ustulatus*) very abundant,
474 despite the presence of nearby potential source populations. Our target list included
475 several NNS already reported from the open coast in California, suggesting some
476 propensity to colonize outer coasts. It is of course possible these NNS are present at our
477 study sites, but not sufficiently abundant for us to have detected them. Nonetheless, it
478 appears that the general pattern of relatively few invaders being found on the open coast
479 continues to hold for our study region. This concurs with an older but more
480 comprehensive survey of macroinvertebrates, algae and fishes from the intertidal zone in
481 our study region, which found only five NNS (Zabin et al. 2013, actually reported as
482 four, as *C. peregrina* was not recognized then as a non-native).

483 Our survey data also suggest that in general the NNS previously reported from
484 our study region are not spreading rapidly. Notably, the sponge *Hymeniacidon sinapium*
485 was found only from the same two sites where researchers noted it in 1997 (although it
486 was not found in surveys of these sites in the 1970s, Zabin et al. 2013, their Digital
487 Supplement 1) and only in very small patches. *Bugula “neritina”* was reported from one
488 site in our current study compared with two sites in earlier surveys in our study area
489 (Zabin et al. 2013, their Digital Supplement 1, biogeographic status reported as
490 “unknown”).

491 *B. “neritina”* has been reported from southern to central California waters since
492 the early 20th century (Robertson 1905). Molecular and biochemical work points to two
493 types (Davidson and Haygood 1999). While there is some evidence that one type (Type
494 D) may be native to California (Fofonoff et al. 2017), Type S is considered a worldwide
495 NNS likely transported on ships and in ballast water, given its abundance in shallow bays
496 and on floating docks (Davidson and Haygood 1999). Both have been reported from
497 northern California rocky intertidal zones (Davidson and Haygood 1999), and without
498 genetic analysis, it is unclear which we found.

499 Two other taxa showed no evidence of increasing in frequency or area. We found
500 the brown alga *C. peregrina*, at only one of our study sites, while earlier studies report it

501 as common (Zabin et al. 2013, their Digital Supplement 1). We found this species in
502 summer only, and most of our surveys were conducted in fall, suggesting possible
503 seasonal variation in abundance and detection. We did not find the sponge *Halichondria*
504 *bowerbanki*, which had been found in a single location (Soquel Point) in earlier surveys
505 (Zabin et al. 2013, Supplement 1).

506

507 *Invasions within the Monterey MPA network*

508

509 Within the Monterey area, *Watersipora* was recorded more frequently at sites closer to
510 the Monterey Harbor. Additionally, of the eight sites surveyed in the Monterey area, the
511 site just adjacent to the harbor, Breakwater Cove, appears to have the most NNS, with
512 two of our target taxa recorded from the subtidal and three from the intertidal (Table 4).
513 While one explanation for these observations is that the harbor is a major source of NNS,
514 we also note that the sites closest to the harbor are the most protected from waves, which
515 may make these locations more suited for these typically calm-water species. It is most
516 likely that both factors, abundance of propagules and wave protection, contribute to the
517 observed pattern.

518 It is difficult to predict how extensively *Watersipora* might spread, much less its
519 potential impacts, in the Monterey area. The extent of the bryozoan's current distribution
520 in the area is not known. While we did not find it at sites west or south of Lovers Point in
521 the current study, SIL photographed it in 2008 just south of our southernmost site, Pt.
522 Lobos, and in 2015 a recreational diver provided us with a photograph taken from a kelp
523 forest "somewhere between Big Sur and Morro Bay" (R. Roberts 2015 perscomm).
524 Clearly *Watersipora* is able to colonize natural substrate in areas far from the protected
525 Breakwater site. The abundance of *Watersipora* in the area has been dynamic, as the
526 student-collected data from Hopkins Marine Station indicate. Additionally, large foliose
527 colonies can form over the course of 3 to 4 months and then disappear (JW, SIL unpubl
528 data) making it easy to miss in a survey at a single time point. *Watersipora* has been
529 relatively well studied in calm-water environments, where its effects on other species are
530 variable (Stachowicz and Byrnes 2006; Sellheim et al. 2010; Needles and Wendt 2013).
531 Little is known about its potential ecological impacts in open-coast conditions.

532 *Watersipora* was the only target species detected from sites other than Breakwater
533 Cove in our finer scale Monterey area study. We were surprised that we did not find the
534 kelps *Undaria pinnatifida* or *Sargassum muticum*, given their long presence and
535 abundance in many of the nearby harbors and invasion history on the open coast
536 elsewhere in the state (Zabin et al. 2009; Miller et al. 2011). Another of our target
537 species, *Sargassum horneri*, was also not found. This alga has spread along the open
538 coast from Santa Barbara, California to the southern tip of Baja California, Mexico
539 (Marks et al. 2015). Thermal tolerances may restrict its spread north of Santa Barbara
540 under present conditions, but this may change under future climate scenarios (Marks et
541 al. 2015).

542 Overall, our findings suggest that NNS are not widespread or abundant within
543 this network of MPAs. This generally supports the view of NNS as a relatively minor
544 current threat to native ecosystems. However, the success of *Watersipora* within some of
545 these diverse, iconic rocky shore habitats underscores the potential vulnerability of high-
546 value open coast systems to NNS, particularly at sites near highly invaded harbors.

547

548 *Management considerations for MPAs*

549

550 While it may be difficult to determine which factor or combinations of factors result in
551 colonization of the outer coast by NNS, some of these are worth reviewing in light of
552 management considerations for marine sanctuaries and protected areas globally. In
553 reviewing these considerations, it is important to keep in mind that NNS are a
554 heterogeneous group of organisms, spanning multiple phyla, thus no one single
555 management action can be expected to prevent colonization and establishment or reduce
556 impacts of all NNS (Jeschke et al. 2012).

557

558 1. Vectors. In general, there are fewer vectors that transport NNS to outer coast locations.
559 However, small recreational vessels and fishing boats do travel between international
560 ports and outer coast locations, including remote and relatively pristine areas, and may
561 play a role in the transport of species (Wasson et al. 2001; Floerl and Inglis 2005; Clarke
562 Murray et al. 2011; Ashton et al. 2014; Zabin et al. 2014). Although this is less well

563 documented for marine environments, species also may be transported on the outer coast
564 by recreational users, such as boaters, fishermen, and scuba divers, and researchers on
565 personal gear and equipment (Williams and Smith 2007).

566

567 2. Biotic resistance. Diverse, multi-trophic ecosystems are thought to provide biotic
568 resistance against invasions. Management actions that promote healthy ecosystems that
569 include top predators, consumers, and native foundation species might help promote
570 biotic resistance, although the evidence for this is equivocal. For example, while Albins
571 and Hixon (2013) contend that marine reserves that protect top predators are one
572 potential hope for reducing non-native lionfish – and call such protections “a
573 precautionary and foresighted management approach” to deal with this invasion, other
574 studies show no correlation between predators and lionfish (Hackerott et al. 2013).
575 Williams and Smith (2007) in their meta-analysis of invasive seaweeds suggested that
576 native herbivores do not control non-natives, but they did find some evidence of at least
577 initial biotic resistance in undisturbed algal communities.

578

579 3. Disturbance. Disturbed environments are thought to be more vulnerable to invasion by
580 NNS. Anthropogenic disturbance, including habitat destruction, nutrient or sediment run-
581 off, overharvesting, alteration of temperature, wave, and current regimes might promote
582 NNS (Diez et al. 1999; Sanchez and Fernandez 2006; Williams and Smith 2007). The
583 addition of artificial hard substrates such as seawalls, jetties and oil drilling platforms can
584 also be considered a disturbance and has been linked to the spread of NNS into coastal
585 habitats (Chapman and Johnson 1990; Bax et al. 2003; Bulleri and Airoidi 2005; Page et
586 al. 2006; Dafforn et al. 2015; Simons et al. 2016).

587

588 Researchers are increasingly calling for NNS detection and management to be
589 incorporated into marine conservation planning (Bax et al. 2003; Keller et al. 2009; Otero
590 et al. 2013; Ladd and Collado-Vides 2013; Ardura et al. 2016; Bumbeer and Moreira da
591 Rocha 2016). At the very least, management efforts to protect valued native species and
592 reduce non-natives must be coordinated to avoid situations where NNS are protected
593 because they are in no-take zones (Bax et al. 2003; Burfeind et al. 2013).

594 Clearly an MPA designation alone is not enough to control NNS. Our relatively
595 small study indicates no difference between areas inside of and outside of MPAs, and
596 adds support to several earlier studies. For example, in a review of MPAs in the
597 Mediterranean Sea, Guidetti et al. (2014) found no evidence that these areas were more
598 resistant to invasions. In a meta-analysis of 13 MPAs for which they could find
599 quantitative data on NNS inside and outside of marine reserves, Burfeind et al. (2013)
600 reported no effect of reserves on NNS in seven cases, and enhanced abundance of NNS in
601 six cases. It is also not always clear which management actions might be effective. For
602 example, MPAs that protect herbivorous fish have been found to lead to more
603 encroachment of *Caulerpa racemosa* in the Mediterranean, although some measure of
604 resistance is evident where sea urchins are protected (Tamburello et al. 2014).
605 Interactions between invasions and other anthropogenic stressors may be particularly
606 pertinent and require a better understanding. As an example, spread of *C. racemosa* was
607 greatest in areas where anchor damage and heavy grazing by herbivorous fish were both
608 present (Tamburello et al. 2014).

609

610 *Conclusions*

611 The relative paucity of NNS in our study area contrasts strongly with many open-
612 coast Southern California locations, where several NNS, particularly seaweeds, are
613 widespread and abundant (Miller and Engle 2009; Preisler et al. 2009; Miller et al 2011;
614 Kaplanis et al. 2016). The reasons for this difference are not known. Greater invasion
615 success in Southern California has been attributed to warmer waters, lower wave energy,
616 and greater retention of propagules within the Southern California Bight system, as well
617 as greater amounts of anthropogenic disturbance and lower native species diversity
618 (Preisler et al. 2009). The changes in water temperature and current patterns that result
619 from periodic oceanographic shifts such as El Nino-Southern Oscillation, Pacific Decadal
620 Oscillation and/or to global climate change, have been linked to northern range
621 expansions of native species (Sagarin et al. 1999; Schultz et al. 2011; Leising et al. 2015).
622 More range expansions of native and non-native open-coast species may occur under
623 global climate change scenarios (but see Hilbish et al. 2010), and the question remains
624 whether the pattern of fewer NNS on the open coast in central and northern California

625 will change over time. Our finding of *Watersipora* on the open coast is particularly
626 noteworthy in this regard, as the bryozoan is generally restricted to calm-water
627 environments globally. This suggests that other calm-water species could spread to the
628 open coast, even after a long lag time in harbors as *Watersipora* did on our coast.

629 While the vectors – both anthropogenic and natural – that transport NNS operate
630 at a scale larger than most MPAs, managers may be able to reduce local stressors (Ladd
631 and Collado-Vides 2013) or local vectors (Ardura et al. 2016) and increase protection of
632 native ecosystems. Thus, an improved understanding of which factor(s) allow
633 colonization and spread of NNS to these outer coastal habitats and protected areas is a
634 high priority for invasion ecology and ecosystem management.

635

636 **Compliance with Ethical Standards**

637

638 Conflict of interest

639 The authors declare that they have no conflicts of interest.

640

641 Animal ethics

642 All animals and plants have been sampled according to state and federal guidelines, and
643 all required research permits and permissions were obtained.

644

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658

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