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4	Article type : Special Section
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7	Integrated Pest Management for Fouling Organisms on Boat Hulls
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26	Running head: Management of hull biofouling
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28	Abstract
	This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may

not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u>. Please cite this article as <u>doi:</u> <u>10.1002/NAFM.10360</u>

29 Boating is a major vector for aquatic invasive species that cause significant economic and 30 ecological impacts, necessitating biofouling control that goes beyond simply maintaining boat 31 operations. However, new regulations restricting the use of antifouling paints, a common 32 control tactic along with hull cleaning, have not considered the consequences to invasive 33 species management. As a result, there is a critical need for a biofouling control strategy that 34 both protects water quality and minimizes invasive species transport. We compared 35 recruitment of fouling organisms to experimental plates: 1) treated with hull coatings after 1 36 month and, for copper-based paint, after 1, 3, 6, and 12 month submersion times, 2) after 37 application of California's in-water hull cleaning practices, and 3) among locations within and 38 between geographically separated harbors. Copper-based paint was initially effective at 39 reducing fouling, but lost effectiveness over time and was fouled heavily within 12 months. On 40 plates with copper-based paint, non-native species typically recruited first and facilitated the 41 recruitment of other species. Nontoxic coatings were readily fouled and invasives, Watersipora 42 subatra and Hydroides spp., settled more often on the epoxy and/or slick coatings. Recruitment 43 was higher in the harbor in the warmer water region. Depending on the harbor, W. subatra, 44 *Ciona* spp., and *Filograna implexa* recruitment was correlated with water flow and/or the 45 presence of conspecifics on the docks. Strong seasonal recruitment was evident for Ciona spp., 46 F. implexa and Bugula neritina. Algae dominated light-exposed surfaces and invertebrates 47 dominated shaded surfaces of plates. California's hull cleaning practices did not stimulate 48 fouling, which contradicted findings from elsewhere. Our findings informed the development of 49 an integrated pest management framework for biofouling control on boat hulls adaptable to 50 different regions and boater needs. This novel approach balances effective boat operations and 51 protection of ecosystem health while simultaneously addressing water quality and invasive 52 species transport.

53

54 Introduction

Fouling organisms, biota that attach and grow on manmade surfaces, such as boat hulls, pilings,
 cables, pipelines and docks, have been long considered pests by many who work in or enjoy
 aquatic habitats. Biofouling is an accumulation of these organisms, including a variety of soft

and hard sessile species of algae and invertebrates. When these marine and freshwater fouling
 organisms attach to and accumulate on boats they interfere with hydrodynamics. This creates
 frictional drag that slows vessels, diminishes ship maneuverability, and reduces fuel efficiency,

61 increasing costs and hydrocarbon emissions (Champ 2000; Yebra et al. 2003; Schultz 2007).

62 Thus, controlling fouling organisms is critical for boat maintenance.

63

64 The need to control biofouling on boats has intensified with the identification of boat hulls as a 65 primary vector for aquatic invasive species (AIS). AIS can affect humans and the environment, 66 causing economic and/or ecological impacts as have been reported worldwide (Pimentel et al. 67 2000, 2005; Ehrenfeld 2010). Historically, ships have been considered the main vector for 68 moving fouling species across oceans to large international ports. Boats are now recognized as 69 a vector for spreading non-native species from large ports to small craft harbors, and among 70 inland lakes and reservoirs (Johnson et al. 2001; Wasson et al. 2001; Floerl et al. 2009; Ferrario 71 et al. 2017). Countries such as Australia, New Zealand (NZ), Canada and the United States (US) 72 (e.g., California, Hawaii) propose to limit new introductions of saltwater AIS from boating, 73 fishing and other recreational activities because of their detrimental impacts on human and 74 natural systems (Godwin 2005; CDFW 2008; Australian DAWR 2015; Maritime NZ 2015; 75 Canadian Minister of Justice 2015; McKenzie et al. 2016). Several regions, including many US 76 states, already have implemented regulations making it illegal to transport freshwater AIS, such 77 as aquatic weeds and Eurasian mussels, via boats and trailers (e.g., State of Michigan 2019). 78

79 Chemically active coatings known as antifouling paints are used to deter biofouling on hulls of 80 recreational and commercial boats and ships. Toxic copper-based paints are currently used as a 81 primary biofouling control method around the world (Piola et al. 2009). However, there are 82 growing concerns about the impacts of these toxic paints on water quality and ecosystem 83 health. In particular, leaching of copper from boat hulls has contributed to elevated levels of 84 dissolved copper in some saltwater habitats, including several harbors in California (e.g., Schiff 85 et al. 2007; Singhasemanon et al. 2008; Kiaune and Singhasemanon 2011). These elevated 86 copper levels are known to affect the health of many marine organisms (Martin et al. 1981;

87 McIntyre et al. 2008; see also review by Eklund and Watermann 2018). Nonetheless, some non-88 native fouling organisms have been found to tolerate elevated copper levels (e.g., Floerl et al. 89 2004; Crooks et al. 2011; see also review by Lande et al. 2011; Osborne et al. 2018). Piola and 90 Johnston (2006) reported a high prevalence of non-native species in a copper-polluted harbor, 91 thereby representing a high proportion of the fouling organisms available to attach to vessels in 92 the harbor. Dafforn et al. (2008) also suggested that boats with copper-based coatings may 93 facilitate transport of these non-native, copper tolerant fouling species. These findings suggest 94 that copper-based antifouling paints may be increasing the risk of transporting non-native 95 species via boat hulls, potentially impacting ecosystem health, and adding to the concerns 96 about using these paints for biofouling control.

97

98 Negative impacts of copper-based antifouling paints on water quality and ecosystem health 99 have resulted in governmental actions by several domestic and foreign agencies, with 100 subsequent effects on boat owners and boating industries around the world, particularly in the 101 US, Australia, NZ, and the Baltic and North Seas. In the US, actions include restricting allowable 102 copper levels in and leaching rates of antifouling paints (Washington State Legislature 2011; 103 CDPR 2014a, 2014b; US EPA 2010), and setting a state (California) standard for allowable 104 concentration of dissolved copper in marine waters (US Environmental Protection Agency 105 2000). Reductions in copper emissions from antifouling paints are required in boat basins that 106 exceed the standard (e.g., CRWQCB-SDR 2005, 2006). Further, the US Environmental Protection 107 Agency (EPA) (2016) is examining national water quality criteria for copper in estuarine and 108 marine waters. In the Baltic Sea, a multi-national, interdisciplinary program is being conducted 109 by a northern European consortium of academic, government and private research 110 organizations to reduce toxins from antifouling paints used on recreational boats (Change 111 2014). Some countries already regulate copper antifouling paints on smaller boats operating in 112 saltwater and freshwater (Sweden, Eklund and Karlsson 2010; Denmark, Danish EPA 2015). 113

114 Integrated Pest Management Strategy for Hull Fouling

115 New and planned regulations on copper emissions will certainly help address water quality 116 issues arising from copper-based antifouling paints on boats in regulated areas. However, they 117 do not consider the potential consequences of AIS transport and biofouling control more 118 broadly. An adaptive Integrated Pest Management (IPM) approach, using a combination of 119 tactics (chemical, physical, cultural) for multiple pest life stages, can inform development of an 120 effective and balanced fouling control strategy that simultaneously considers boat operations 121 and ecosystem health, both water quality and AIS. Development of this type of control strategy 122 requires understanding the complexity and interaction of factors that influence the settlement, 123 growth, reproduction and accumulation of fouling organisms on boat hulls.

124

125 To develop an IPM framework for biofouling control we investigated recruitment responses of 126 fouling organisms to select factors. Our research objectives were to: 1) Assess the influence of 127 hull coatings on recruitment of fouling organisms, 2) Assess the influence of aging copper-based 128 antifouling paint on recruitment of AIS and native fouling organisms, 3) Experimentally evaluate 129 the influence of standard hull cleaning practices used in California on the accumulation of 130 biofouling on boat hulls, and 4) Evaluate temporal and spatial recruitment patterns to 131 determine the potential effects of time of year, location among and within harbors, and 132 environmental factors on the recruitment of fouling organisms to boat hulls.

133

134 By addressing these objectives we gained insights for controlling biofouling on boats and in 135 harbors. We identified settlement preferences (Crisp 1984; Pawlik 1992) of fouling organisms 136 for different types of hull coatings and ages of copper-based antifouling paint, information 137 needed to determine which fouling species required control. We also evaluated the efficacy of 138 California's in-water hull cleaning practices for reducing fouling that was questioned following 139 reports that it stimulated attachment of fouling organism in Australia (Floerl 2002; Floerl et al. 140 2005). Evaluation of environmental variables that may influence fouling, including water 141 temperature (Stachowicz et al. 2002; Scheibling and Gagnon 2009; Sorte et al. 2010), salinity 142 (Lambert and Lambert 2003), water motion or flow (Leichter and Witman 1997), shading 143 (Glasby 1999a; Miller and Etter 2008), proximity to the seafloor (Glasby 1999b) and the

presence of nearby conspecifics (Jensen and Morse 1984; Minchinton 1997), enabled us to develop predictions about the intensity and timing of fouling at locations within and among harbors. This in turn helped us to evaluate how various fouling control tactics might be incorporated into a hull fouling control strategy.

148

149 Based on our key findings and those of related work, we developed an IPM framework for 150 managing hull fouling that considers boat and harbor operations, water quality and invasive 151 species. Aspects of this framework focus on reducing spread of non-native fouling AIS 152 specifically, as these species are highly abundant in harbors worldwide (Cohen et al. 2001, 153 2005; Paulay et al. 2002; Hewitt et al. 2004), contributing substantially to the available fouling 154 assemblages that accumulate on boat hulls. AIS control is thus essential for overall fouling 155 control on boat hulls to minimize drag, extend the service life of hull coatings, and maintain the 156 integrity of native ecosystems where boats are taken. Although our work concentrates on 157 saltwater conditions of specific regions, the resulting IPM framework for hull fouling can be 158 broadly applied to other locations, including freshwater systems, if it is adjusted to local 159 conditions and fouling biota. The general IPM fouling control framework and associated 160 information is intended to inform technically, ecologically and economically sound decision and 161 policy making for controlling fouling on boat hulls while maintaining boat operations, protecting 162 water quality and minimizing the spread of AIS.

163

164 [A]Methods

We focused our study on saltwater boating, where boats typically travel from location to location without being removed from the water. This differs from freshwater boating where boats often are hauled out of the water and transported on a trailer to other locations. We further focused our study on small recreational and commercial vessels and did not include saltwater ships (large vessels), such as those used in commerce and the military, as they differ in operational parameters and economics that influence the approach required for fouling control. We also concentrated on factors influencing fouling for boats that rarely move from their harbors, as our earlier research indicated that this represents half of California boaters(Johnson and Fernandez 2011).

174

175 [C]Study sites.—Our field studies were conducted in two small craft harbors on the southern 176 California coast: Santa Barbara Harbor (SBH), Santa Barbara (34.405811, -119.691254); and 177 Shelter Island Yacht Basin (SIYB) of San Diego Bay, San Diego (32.711111, -117.235278) (Fig. 1). 178 These harbors are frequented by commercial and recreational boats in Santa Barbara and by 179 recreational boats in San Diego. These two harbors are located, respectively, in the northern 180 and southern portions of the Southern California Bight within two marine biogeographic 181 provinces. The Santa Barbara region is within the "California Transition Zone" where warm and 182 cold waters of the Californian and Oregonian provinces mix, whereas the San Diego region is 183 influenced by the warm waters of the San Diegan province (Dawson 2001).

184

185 The effects of hull coating, time of year, location (among and within harbors), and 186 environmental variables on recruitment of fouling organisms were examined at 28 stations in 187 the two study harbors. Stations 1 through 16 were in Santa Barbara Harbor (SBH) (Fig. 1a) and 188 Stations 17 through 28 were in Shelter Island Yacht Basin (SIYB) (Fig. 1b). For most analyses, the 189 SBH stations were further grouped into four locations along a gradient from the inner to outer 190 harbor across the width of the harbor. The SIYB stations also were grouped along a gradient 191 from the inner to outer basin in association with three separate marina locations: inner, Half 192 Moon Anchorage (HMA) (stations 17-20), middle, Southwestern Yacht Club (SWYC) (stations 21-193 24) and outer, Kona Kai Marina (KKM) (stations 25-28).

194

Two other field studies were conducted at a subset of the above stations. We investigated the effects of aging of copper-based paint on fouling at two locations in SIYB: at the inner (HMA) (Stations 17-20) and outer basin (KKM) (Stations 25-28) (Fig. 1b). An assessment of hull cleaning methods on accumulation of fouling was conducted at three locations: one in SBH (stations 13-16) and two in SIYB [HMA (Stations 17-20) and KKM (Stations 25-28)] (Fig. 1). 201 [C]Experimental set-up.–We conducted these studies on floating docks in the harbors and 202 marinas described above. At each station, we deployed a PVC frame with 15 cm x 15 cm 203 fiberglass experimental plates attached vertically to the inside of the frame (Fig. 2). Plates were 204 randomly assigned to positions along the frame. The side of the plate facing out into the slip 205 represented the 'front' and the side facing the dock was the 'back.' Frames were attached to 206 the northern (SBH) or the northwestern (SIYB) facing side of the floating docks, with the plates 207 at a depth of 1 meter below the surface of the water where hull cleaners have noted extensive 208 fouling. Four replicate frames were deployed at each location for each experiment. Prior to 209 attachment of the frame to the dock, fouling organisms were removed from the area directly 210 behind the frames and a small (~ 5 cm) buffer zone around the frames.

211

212 Hull coatings representing typical brands used in California at the time of the study were 213 applied to the experimental plates by a commercial boat repair yard in San Diego. All plates 214 were initially coated with Cook Composites polyester gel base coat (gel or gel coat), as is done 215 on boat hulls prior to application of toxic antifouling paints and nontoxic (nonbiocidal) coatings. 216 Depending on the experiment (Table 1), treatment-coatings were applied over the initial gel 217 coat. The treatment coatings were: 1) copper-based antifouling paint, Interlux Epoxy Modified 218 Antifouling ('copper'); 2) nontoxic, ceramic-epoxy, CeRamKote Marine ('epoxy'); 3) nontoxic, 219 siliconized epoxy, Eco-5 Marine ('slick'); and 4) nontoxic, gel, Cook Composites polyester ('gel'). Note, herein we refer to nontoxic, siliconized epoxy coatings as 'slick' coatings, not 'foul-220 221 release' coatings; terminology appropriate for the recreational boating milieu. Coatings were 222 black in color because this was the only available color common to the types of paints and 223 coatings used for the studies.

224

The size of the experimental frames, the number of plates on each frame, the type of coating on the plates, and the duration and time frame of the experiments differed for each field experiment (Table 1; Fig. 2). Details of each experiment follow.

228

Hull Coatings: The evaluation of the effect of hull coating on recruitment of fouling organisms
 included four treatment plates, one for each type of coating described above (one toxic and
 three nontoxic coatings) (Fig. 2a). The nontoxic gel coat plates in this experiment also were
 used for the Time of Year and Location studies (see below).

Aging Copper-Based Antifouling Paint: The assessment of the effect of aging of copper-based paint on the recruitment of fouling organisms on plates included three experimental plates with the same copper-based antifouling paint (Interlux Epoxy Modified Antifouling paint) used in the Hull Coating Experiment (Fig. 2b). Each plate was assigned to one of three submersion time treatments: 3, 6 or 12 months.

239

233

240 Hull Cleaning: The evaluation of the effect of hull cleaning methods on accumulation of fouling 241 organisms included three sets of three plates (nine plates total) with three coating types and 242 three cleaning treatments (Fig. 2c). The same coatings (copper, epoxy and slick applied over a 243 gel-coat base) used in the other experiments were used for this experiment. Three cleaning 244 treatments, 1) frequently cleaned, 2) cleaned once and 3) not cleaned (new), were applied to 245 plates on each frame. Plates undergoing the 'frequently cleaned' treatment were submerged 246 and cleaned frequently for a three-month period. At the same time, the 'cleaned once' 247 treatment plates were allowed to continually accumulate fouling over the three-month period. 248 At the end of the third month, plates from both of these treatments were cleaned and returned 249 to the water along with a third treatment consisting of a set of new plates ('not cleaned') that 250 had not previously been submerged in the water. None of the plates were cleaned during the 251 fourth month when fouling was allowed to accumulate on the treatment plates. The amount 252 and type of fouling were evaluated on the front side of the plates in each treatment at the end of the fourth month. 253

254

California best management practices (BMPs) for hull cleaning, developed by the California
 Professional Divers Association (CPDA), were followed whenever plates were cleaned in this
 experiment. The least pressure and softest cleaning tool were used first (Johnson and Gonzalez

2004). Pressure was gradually increased and more abrasive tools were used as needed, with plates cleaned in a container of saltwater. In accordance with the California BMPs for warm water areas (i.e., San Diego), plates in the 'frequently cleaned' treatment were cleaned every two weeks for the nontoxic coated plates and every three weeks for the plates with copperbased antifouling paint. The same BMPs were also used for the 'cleaned once' treatment, but (as noted above) these plates were cleaned only once at the end of the three months.

265 During each cleaning, the type of fouling growth was rated visually for each plate, whether 266 cleaned or not, using the Five-Point Scale of the California BMPs (Johnson and Gonzalez 2004). 267 Light "silting" (biofilm) represented the lowest rating (1) and substantial hard growth 268 represented the highest rating (5). For all plates that were cleaned, we also recorded the 269 cleaning tool and effort required to remove the fouling growth in accordance with the Five-270 Point Scale. In this case, the lowest rating (1) was defined by the least abrasive tool and the 271 lightest pressure, with the highest rating (5) indicating use of the most abrasive tool and highest 272 degree of physical effort.

273

Temporal and Spatial Recruitment Patterns: Our studies evaluating time of year, location and
 environmental factors used the same frames and gel-coated plates as used in the Hull Coating
 Experiment. To assess temporal and spatial recruitment patterns we analyzed monthly
 recruitment of fouling organisms to the gel-coated plates for 15 months and 12 months,
 respectively.

279

We measured several environmental variables at all stations including water temperature, salinity, water flow, light, water depth and the abundance of nearby conspecifics. These data were used to explore potential relationships between environmental variables and the recruitment of fouling organisms. Water temperature was measured with continuously recording temperature loggers (HOBO[™]) attached to the experimental frames deployed at each station for the Hull Coating Experiment. The data loggers recorded water temperature every 15 minutes. The data were downloaded monthly. Surface salinity was measured weekly at each 287 station using a temperature-compensated refractometer. We also assessed relative differences 288 in water motion (flow) among stations by measuring the dissolution rate of SLOD[™] cards --289 slow-dissolving, gypsum plaster molded to a standard size and fixed to a base -- that also were 290 attached to the experimental frames (Hart et al. 2002). SLOD[™] cards were deployed and 291 retrieved monthly. We used plate side (front - facing out, or back - facing the dock) as a proxy 292 to evaluate the influence of light level (shading) on recruitment of fouling organisms on the gel-293 coated plates. Water depth was measured at each station since proximity to the bottom could 294 influence turbidity and the availability of sediment-bound contaminants. Water depth at each 295 station is expressed as a "relative depth": the deviation in depth from the overall mean depth. 296 The abundance of nearby conspecifics, which may attract settlers or provide larvae, was 297 assessed by photographing three 15 cm x 15 cm quadrats (photoplots) situated on the dock 298 floats at each station prior to deploying the experimental frames.

299

[C]Sample retrieval and analysis.-Upon collection from frames (see Table 1 for schedule), all
 plates were photographed, both front and back, and then placed in a plastic Ziploc[™] bag that
 was filled with air to protect samples from being crushed. Bags were placed in large
 Tupperware[™] containers and transported in a chilled cooler to the laboratory where they were
 frozen for subsequent processing and analysis (see Sample Analyses). One exception to this was
 the plates from the Hull Cleaning Experiment, which underwent a different process. Details of
 specific protocols for each experiment follow.

307

308 Hull Coating and Aging of Copper-Based Antifouling Paint: We visually identified and measured 309 the proportional cover of all sessile organisms attached to the front and back of the plates using 310 point-contact sampling (Underwood and Anderson 1994). A clear plastic grid with 50 randomly 311 distributed holes was placed over each plate and a 1 mm diameter pin was inserted through 312 each hole to contact the organism on the plate below it. Every organism the pin touched was 313 identified and recorded. To calculate proportional cover of a species, the number of pin 314 contacts was then multiplied by two. In cases where species overlapped and layering occurred 315 there was more than 100% total cover on a plate. Counts of non-colonial species also were

recorded. Organisms growing within 0.4 cm of the edge of the plate were not analyzed to avoidpotential influences by conditions that might occur only near the edge.

318

319 Species/taxa on the plates were identified to lowest possible taxonomic level, with voucher 320 samples sent to appropriate taxonomists for confirmation of identifications. In some cases, it 321 was only possible to identify organisms to the level of genus as the species has not been fully 322 resolved by taxonomists (Table A.1, A.2). We grouped the polychaetes, Hydroides elegans and 323 *H. gracilis,* because it is difficult to distinguish between these species without microscopic 324 inspection of each individual worm. A subsample of this worm complex was analyzed and a mix 325 of species was present, with far more *H. elegans* (non-native) present than *H. gracilis* (native) in 326 the sample. However, it is unknown whether this was the case for all colonies of these worms 327 that we encountered. We also grouped *Ciona intestinalis* and *savignyi*, two non-native solitary 328 tunicates. When possible, each species recorded on the plates was categorized by origin (native, non-native, cryptogenic) based upon the California Aquatic Non-native Organism 329 330 Database that is managed by California Department of Fish and Wildlife (CDFW 2011). We 331 categorized *Diplosoma listerianum* as non-native instead of cryptogenic, however, because of 332 conclusions detailed in Ruiz et al. (2000).

333

Hull Cleaning: All plates were cleaned and the fouling growth, cleaning tool and cleaning effort
were recorded at the end of the experiment as described above. In addition, we assessed the
amount of fouling (accumulated biomass) on each plate by collecting all the fouling growth that
had accumulated over the one-month period (between months three and four) at the end of
the experiment. The collected fouling growth was taken to the laboratory for processing.
Samples were filtered through a Whatman Cat No 1004 090 filter (#4 paper filter), dried in a
drying oven at 15.5°C for 48 hours, and weighed to the nearest 0.0001 grams.

341

342 Temporal and Spatial Recruitment Patterns: Annual means were calculated for water

343 temperature, salinity and SLOD[™] card dissolution rate. The composition and proportional cover

344 of macroalgae and invertebrates attached to the docks was determined from the photoplots by

projecting the image and scoring contacts on 100 uniformly spaced points (similar to how theplates were scored).

347

348 [C]Statistical analysis.—The statistical analyses were conducted using Excel, SAS 9.2, SYSTAT 13
 349 and SPSS 19. Details of specific analyses for each experiment follow.

350

351 Hull Coating: To evaluate the effect of hull coating on fouling, we compared the recruitment of 352 organisms among three nontoxic hull coatings (epoxy, slick and gel) for the two different 353 harbors (SBH, SIYB) using a multivariate analysis of variance (MANOVA), with individual 354 species/taxa as the dependent variables. The toxic coating type (copper-based antifouling 355 paint) was not included in these statistical analyses because the data for this coating violated 356 the assumptions required for the analysis. We focused our analysis on non-native, cryptogenic 357 or unresolved taxa as they represented the dominant organisms. We constrained the analysis 358 to better meet the mathematical assumptions of MANOVA by excluding rare taxa, which kept 359 the number of variables (taxa) less than or equal to the number of stations. To be included, a 360 taxon needed to occur on at least 45% of the plates and the average annual proportional cover 361 needed to exceed 0.010 (1%). All proportional cover data were arcsine-transformed prior to 362 analysis. Individual count data were log-transformed. Analyses were run using SAS 9.2.

363

364 Aging of Copper-Based Antifouling Paint: We analyzed the effect of aging of copper-based 365 antifouling paint on fouling of experimental plates using the proportional cover of all sessile 366 organisms and individual counts of solitary organisms, measured as described above. In this 367 experiment, data from the front and back surfaces of the plates were combined due to the low 368 occurrence and coverage of most species encountered. Differences in the proportional cover of 369 non-native and native species after 12 months at each location were analyzed using the paired 370 Student T-test on arcsine-transformed data. Because the data for the two shorter submersion 371 times (3 and 6 months) violated the assumptions required for statistical analyses (normally 372 distributed data, homogeneity of variance), only general trends are discussed for these data. 373 Analyses were run using SAS 9.2.

374

Hull Cleaning: The effect of cleaning practices on fouling biomass was analyzed using KruskalWallace non-parametric rank test to evaluate differences in rankings of fouling growth type,
cleaning tool and cleaning effort among locations, coating type, and cleaning treatment. To test
for differences in accumulated biomass (amount of fouling) among locations, coating type and
cleaning treatment we used Analysis of Variance (ANOVA). Biomass data were log (x+1)
transformed prior to analysis (Zar 1999). Analyses were run using SAS 9.2.

381

382 Temporal and Spatial Recruitment Patterns: The effect of time of year on recruitment of fouling 383 organisms was described by the dispersion in recruitment computed as the coefficient of 384 variation (CV) in monthly cover during the 15 months of the study. The influence of location 385 and environmental parameters on fouling including the effects of plate side (front versus back) 386 and location within the harbors (outer to inner harbor) on the abundance (as proportional cover) of the more common algae and invertebrates were explored using multivariate analysis 387 388 of variance (MANOVA). Plate surface and location were designated as fixed factors and the 389 cover of algal and invertebrate taxa as the response variables. The assumptions of normality 390 and homogeneity of variances were explored using Shapiro Wilks' test and Levene's test, 391 respectively. The tests showed that these assumptions were typically violated for ~25% of the 392 taxa within each location x side combination. However, MANOVA is generally considered robust 393 to violations of these mathematical assumptions (Lindman 1974, Bray and Maxwell 1985). If the 394 multivariate test statistic Wilks' λ was significant (P<0.05), significant effects of side and 395 location for individual taxa were identified using univariate F-tests. MANOVA analyses were run 396 using SYSTAT 13 and SPSS 19. Proportional cover data were arcsine-transformed (p'= arcsine 397 Vp) prior to analysis as recommended by Zar (1999).

398

We used correlation and regression analyses to examine relationships between the annual
means of environmental variables for each station and linear distance from the outer to inner
harbor. Distance was measured for each station from an arbitrary point established in the outer
harbor (SBH: 34.405811, -119.691254; SIYB: 32.711111, -117.235278, Fig. 1). Within each

harbor, we explored potential correlation among values of water temperature, salinity, flow,
and water depth measured at each station. For variables that were cross-correlated, we
selected the variable that showed the fewest significant correlations with the other variables or
those that we viewed as most likely to help explain observed patterns for use in subsequent
correlation and regression analysis.

408

For those invertebrate taxa showing significant location effects with MANOVA, we used correlation and regression analysis to explore potential relationships between monthly mean cover of these taxa averaged across 12 months, and the measured environmental variables, which included the cover of the taxa of interest on the dock. Only those taxa that could be satisfactorily identified in the photoplots were used in this analysis. Correlation analyses were run using SYSTAT 13.

415

416 [A]Results

417 [B]Hull coatings

10 C

418 More than 35 taxa of fouling organisms from 8 phyla recruited to the plates with new nontoxic 419 coatings and reached high cover over one-month intervals at both harbors (Table A.1). When all 420 taxa are included, percent cover of fouling organisms on the plates with nontoxic coatings over 421 the short time intervals was quite high averaging 71.3% to 91.4% with more fouling observed at 422 the southern harbor. Dominant species on the experimental plates with nontoxic coatings 423 included a few taxa of unresolved taxonomy and several AIS (Figs. 3-5). Nearly half of the cover 424 on plates at both harbors consisted of one or two algal taxa, Enteromorpha and Cladophora, 425 and tube worms in the family Spirorbidae (Figs. 3, 4). Spirorbid tube worms were very dense at 426 the southern harbor as compared to the northern harbor over the three coating types (Fig. 4). 427 The dominant non-native species observed on the plates included branching and encrusting 428 bryozoans, Bugula neritina, Watersipora subatra (formerly W. subtorquata in our region; Vieira 429 et al. 2014), and Cryptosula pallasiana, a tube worm, Hydroides elegans, the solitary tunicates 430 *Ciona* spp., and the colonial tunicates, *Diplosoma listerianum* and *Botrylloides violaceus* (Fig. 3). 431 At the southern harbor (SIYB), two additional primary invertebrate species were observed on

the plates: the tube worm, *Filograna implexa*, and the colonial tunicate, *Botryllus schlosseri* (Fig.3b).

434

435 At the southern harbor (SIYB), recruitment of fouling organisms was significantly affected by 436 the type of nontoxic coating on the plate for both colonial (proportional cover) (λ value, 0.327, 437 F = 2.68, P < 0.001; Fig. 3b) and non-colonial (counts) species (λ value, 0.663, F = 2.91, P = 0.006; Fig. 4b). Recruitment of the invasive *W. subatra* was significantly higher on plates with epoxy 438 439 and slick coatings as compared to the plates with only gel coat (p < 0.001). Also, recruitment of 440 Hydroides spp. (H. elegans and H. gracilis) was significantly higher on the epoxy nontoxic 441 coating compared to the slick coating (proportional cover, P = 0.022; counts, P = 0.008; Figs. 3b, 442 4b). At the northern harbor, recruitment was lower overall compared to the southern harbor, 443 and it was not significantly affected by type of coating for either colonial (proportional cover) (λ value, 0.684, F = 1.06, P = 0.395; Fig. 3a) or non-colonial (counts) species (λ value, 0.904, F = 444 0.89, *P* = 0.523; Fig. 4a). 445

446

Fouling was extremely limited on plates with copper-based antifouling paint submerged in both
harbors over one-month intervals (Tables A.2). Fouling on these plates consisted of just a few
individuals or very small colonies of a few species of tube worms (including the non-native *Hydroides elegans*) and sabellid worms, a couple of algal taxa of unresolved taxonomy, one
non-native tunicate (*D. listerianum*) and one cryptogenic tube-building amphipod
(*Laticorophium baconi*).

453

454 [B]Aging of Copper-Based Antifouling Paint

Over the 12 months of the experiment, twenty-two different organisms from six taxa were detected on the plates with copper-based antifouling paint (Table A.2). Almost half (45%) of these organisms were rare, occurring on only one plate for a single submersion time at one or both locations at the southern harbor. Several other fouling organisms were more common, occurring throughout the experiment.

460

Fouling organisms recruiting to the plates with copper–based antifouling paints over
intermediate submersion times (3, 6 months) were primarily AIS, along with two cryptogenic
species (*L. baconi* and *Bowerbankia* sp.) and tube worm (*Spirorbis* sp.) of unresolved taxonomy
(Figs. 6-8). Non-native fouling species appeared earlier than native species on these plates. The
AIS observed on the experimental plates with copper-based antifouling paint at both inner and
outer harbor locations included *H. elegans, F. implexa* (Figs. 7b, c), *B. neritina* (Fig. 6a), *W. subatra* (Figs. 6a, b), D. *listerianum* (Fig. 6b), and *Ciona* spp. (Table A.2).

468

The proportional cover of the principal space occupiers increased substantially over time on the 469 470 experimental plates with copper-based antifouling paint at both locations, with these plates 471 becoming heavily fouled within 12 months of submersion (Fig. 6). The cryptogenic amphipod, L. 472 baconi, occupied the most space at the end of the experiment at both inner and outer harbor 473 locations, with the non-native tunicate, *D. listerianum*, occupying the second and third highest 474 amount of space at the inner (HMA) and outer (KMA) locations respectively. Further, non-475 native species occupied more than twice as much space as native species on plates with 476 copper-based antifouling paint submerged for 12 months at both locations (Figs. 6-8). At the 477 outer location (KKM), proportional cover was significantly greater for the four primary nonnative species compared to the three primary native species (KKM: t = 3.22, P = 0.049). A similar 478 479 trend was evident at the inner location (HMA), although these results were not statistically 480 significant (HMA. t = 2.86, P = 0.065) with only one native species (*Aplidium californicum*) 481 versus four non-native species (D. listeranium, F. implexa, W. subatra and B. neritina) recruiting 482 to these plates.

483

Some species recruited on top of other species. We observed that at times *D. listerianum* recruited on top of the tube mats of *L. baconi*. At six months at one of our southern locations (KKM), we found the native alga species, *Rhodymenia pacifica*, recruited onto the non-native bryozoan, *W. subatra*, rather than the plate itself, with direct recruitment onto the plates with copper-based antifouling paint occurring only after 12 months of submersion. The native bryozoan *Bugula californica* also recruited onto *W. subatra* and directly onto some of the plates

with copper-based antifouling paint, but not until the plates had been submerged for 12months.

492

493 [B]Hull Cleaning

494 Hull cleaning did not stimulate the recruitment of fouling organisms, even during the peak 495 period for their recruitment and growth at our three study locations (Fig. 9). Plates that had 496 never been cleaned or that had been cleaned once accumulated just as much fouling growth as 497 plates that were frequently cleaned using the California BMPs ($X^2 = 2.56$, P = 0.083). We found no difference in the type of fouling among locations ($X^2 = 0.009$, P = 0.995) or cleaning 498 treatments ($X^2 = 0.009$, P = 0.995). Similar types of organisms were found on plates at the three 499 500 locations (SBH, KKM, HMA) whether they were cleaned or not. The type of tool and the amount of effort needed to remove fouling growth also did not vary among locations (tool: $X^2 = 2.01$, P 501 = 0.366; effort: X^2 = 2.49, P = 0.287), with the least abrasive tools and similar light to moderate 502 503 effort used on plates at all three locations. However, plates that were cleaned once or 504 frequently cleaned required a slightly more abrasive tool (rank 2 versus 1) and a little more 505 effort (rank 1 versus 2 or 3) to remove the fouling growth than plates that were new and had 506 never been cleaned (Tool: $X^2 = 17.0$, P = 0.0002; Effort: $X^2 = 6.20$, P = 0.045). A slightly more 507 abrasive tool and moderate effort was typically required to remove a dark green algal film or 508 calcareous organisms. Even though the light calcareous growth was fairly easily removed, some 509 scratches on the plates resulted from the process.

510

A slightly more abrasive tool (rank 2 versus 1) and more effort (rank 2 and 3 versus 1) were required to remove the fouling growth from the plates with nontoxic coatings than from the plates with a copper-based paint (tool: $X^2 = 32.9$, P < 0.0001; effort: $X^2 = 79.9$, P < 0.0001). Significantly less fouling accumulated ($X^2 = 50.8$, P < 0.0001; Fig. 10) and significantly different types of fouling ($X^2 = 107$, P < 0.0001) occurred – slime layer (siltation) versus green algae and light growth of calcareous organisms – on the plates with the toxic antifouling paint as compared to those with nontoxic coatings.

- 519 Fouling was significantly less at the northern harbor (SBH) compared to the two southern
- 520 locations at SIYB ($X^2 = 28.5$, P < 0.0001; Fig. 10). Water temperatures at the time of the
- 521 experiment were higher at the southern location, averaging 21.9° C and 22.2° C at the outer
- 522 (KKM) and inner (HMA) locations respectively as compared to 18.8° C at the northern (SBH)
- 523 524

harbor.

525 [B]Temporal and Spatial Recruitment Patterns

Seasonality was evident at both harbors, but the mean recruitment of all our focal species was more seasonal and less dispersed, as reflected in a higher coefficient of variation (CV) value, at the northern harbor (SBH) (1.8 ± 0.2) compared with the southern harbor (SIYB) (1.3 ± 0.1) (t = 3.685, df = 11, *P* = 0.004). Overall recruitment was lowest during late fall, winter, and early spring. We found strong seasonal recruitment of *F. implexa*, *B. neritina* and *Ciona* spp. on nontoxic coatings over one or more summer months at our study harbors (Fig. 10).

532

533 Spatial variation in recruitment of some taxa was evident within the harbors. At the northern 534 harbor, recruitment of Ciona spp. increased (P = 0.017), whereas recruitment of Watersipora (P535 < 0.001) and Spirorbid sp. (P = 0.044) decreased from the outer to inner locations within the 536 harbor (Fig. 11). At the southern harbor spatial variation in recruitment was evident for five of the 12 taxa, including: D. listerianum (P < 0.001); W. subatra (P = 0.017); Spirorbid sp. (P = 537 538 0.015), Hydroides spp. (P = 0.002), and F. implexa (p < 0.001) (Fig. 12). Recruitment of these 539 taxa increased (F. implexa) or decreased (D. listerianum, Spirorbid sp.) from outer (KKM) to 540 inner (HMA) harbor locations or highest at the intermediate location (SWYC) (W. subatra, 541 Hydroides spp.).

542

The recruitment of many algal and invertebrate taxa was significantly influenced by orientation of the plate surface at both the northern (SBH: $P \le 0.01$) and southern harbors (SIYB: $P \le 0.05$) (Figs. 11, 12). The front side of the plate, facing away from the dock and exposed to light, was colonized primarily by algae (*Cladophora, Enteromorpha*), whereas the back side, that faced the dock and was shaded, had little macroalgae, but was colonized by a suite of invertebratesdominated by ascidians, bryozoans, and tube worms.

549

550 Environmental conditions and the distribution of conspecifics within harbors partially explained 551 the spatial patterns in recruitment documented in our study. Recruitment of three of the 552 fouling taxa (F. implexa, Ciona spp., W. subatra) was influenced by water flow rates. Water flow 553 was negatively correlated with recruitment for both *Ciona* spp. at the northern harbor ($r^2 =$ 554 0.49, P < 0.05; Fig. 13) and F. implexa at the southern harbor ($r^2 = 0.62$, P < 0.05; Fig. 14). The 555 strong, negative response of *Ciong* spp. recruitment to enhanced flow found in a 556 complementary manipulative field experiment supports the hypothesis that water flow can 557 influence the distribution and abundance of this taxon (Santschi 2012). Recruitment of W. subatra was positively correlated with water flow at the southern harbor ($r^2 = 0.54$, P < 0.05; 558 559 Fig. 14). In contrast, at the northern harbor W. subatra recruitment was correlated with the 560 cover of conspecifics on the dock floats ($r^2 = 0.64$, P < 0.05; Fig. 13).

561

562 [A]Discussion

563 An effective IPM strategy to control hull fouling requires tactics that target one or more life 564 stages of these diverse organisms. Such tactics include chemical, physical and cultural 565 approaches that can be used in combination as companion methods. Our research results have 566 implications for applying various fouling-control tactics.

567

568 [B]Chemical Tactics

569 Chemical tactics to control hull fouling include toxic hull coatings and the use of liquid chlorine 570 contained within a slip liner (not a focus of our study). Toxic hull coatings, such as copper-based 571 antifouling paints, are the most widely used chemical tactic for fouling control. They are quite 572 effective at inhibiting recruitment and early survival of fouling organisms. However, we 573 illustrated that they pose a risk for transporting AIS because the effectiveness of the toxic paint 574 diminishes over a relatively short amount of time (within 6 months) and non-native species are 575 among the first to recruit to plates with toxic paint. AIS that recruited to the plates can form 576 large colonies that out compete native species for space and food, particularly in disturbed 577 habitats (Page et al. 2006; Piola and Johnston 2008). Some of the species also can be a nuisance 578 for boaters, as they form calcareous colonies that are difficult to remove from boat hulls. 579 Depending on the species, their removal may result in damage to hull coatings if they are not 580 removed when small and easier to dislodge. Our results add to the evidence of copper 581 tolerance of non-native species documented elsewhere (e.g., Floerl et al. 2004; Crooks et al. 582 2011; see also review by Lande et al. 2011; Osborne et al. 2018) and support the hypothesis of 583 Dafforn et al. (2008) that boat hulls with copper-based antifouling paints may facilitate selective transport of copper-tolerant non-native organisms. 584

585

586 For boat hulls with toxic copper-based antifouling paint that are submerged for periods greater 587 than six months, the risks of spreading AIS may be substantially higher. These boats may 588 contain a number of non-native species that have grown and likely are reproducing (although 589 this was not measured), thereby increasing the chance of spreading them to other areas. 590 Further, the copper-tolerant species may provide a foundation on which other fouling species 591 can settle, thereby enabling less-tolerant species to be carried to new areas more readily than 592 would otherwise be possible (Floerl et al. 2004). Crooks et al. (2011) noted this secondary 593 settlement adaptation among invasive fouling species in San Francisco Bay. We observed that 594 the tube-dwelling amphipod L. baconi tolerated the copper-based paint, and that it may have 595 also facilitated recruitment of a non-native tunicate (D. listerianum). Alternatively, the tube it 596 produced may have protected the amphipod from the toxic effects of the paint and D. 597 listerianum may simply have been overgrowing the tube mats, not using them for "protection" 598 from the antifouling paint. We also documented recruitment of the non-native bryozoan W. 599 subatra, a species known to be a foundation to which other organisms, including AIS, can attach 600 (Floerl et al. 2004). Further investigations of secondary settlement of fouling organisms on 601 substrates with toxic antifouling paint will help elucidate the importance of foundation species 602 for facilitating spread of AIS.

603

604 [B]Physical Tactics

605 Physical tactics for controlling hull fouling include using barriers or changing physical factors 606 that alter settlement or attachment of fouling organisms. Well known physical tactics include 607 storing a boat on a trailer, a lift, or in a slip liner (Culver and Johnson 2012). Nontoxic hull 608 coatings, including the epoxy and slick coatings we tested in our experiments, also represent a 609 physical tactic, albeit less recognized as such. While these coatings are not designed to prevent 610 fouling organisms from settling, their surface characteristics can influence recruitment and/or 611 attachment strength of fouling organisms (Pomerat and Weiss 1946; Crisp 1984; Aldred and 612 Clare 2009; Townsin and Anderson 2009). Another tactic is the physical removal of organisms, 613 by hand or with the aid of mechanical equipment, from the boat via hull cleaning both in and 614 out of the water (sometimes defined as a 'mechanical' tactic).

615

616 Biofouling by certain taxa may be reduced by a boater's application of certain hull coatings. For 617 example, we found the slick coating, but not the epoxy coating, attracted tube worms 618 (Hydroides spp.) in some areas. Theoretically, application of the less preferred epoxy coating 619 would therefore help to reduce hull fouling by these tube worms in those areas. Enhanced 620 nanotechnology that characterizes surfaces is expected to lead to the development of new 621 coatings that consider and exploit settlement preferences of fouling organisms (Callow and 622 Callow 2009). In addition, silicone-based (slick) coatings are designed to reduce the strength of 623 attachment of fouling organisms (Anderson et al. 2003; Townsin and Anderson 2009), 624 something we did not investigate during our study. Often referred to as "foul release" coatings, 625 the weaker attachment results in fouling organisms that are easier to remove and/or slough off 626 when a vessel reaches a certain speed. These coatings were initially developed for use on 627 commercial ships that operate at speeds over 15 knots (Townsin and Anderson 2009). 628 However, Kovach and Swain (unpublished data) found that at least partial sloughing can occur 629 at a speed of only 4 knots, a speed that is reached within harbors. These findings suggest that 630 slick coatings may facilitate removal of at least some fouling taxa on boats at low speeds. This 631 outcome would be good for reducing fouling on individual boats. However, the released 632 organisms, depending on their survival and reproductive state after release, could serve as a 633 source for reseeding boats and docks. This could hinder fouling management or lead to new

introductions and spread AIS, especially if released outside the harbor. The coatings industry is
working to improve the ability of these coatings to slough off slime (Townsin and Anderson
2009), an early fouling stage, which might enhance the usefulness of this physical tactic if fewer
organisms are able to recruit.

638

639 In-Water Hull Cleaning

640 In-water hull cleaning is a companion practice used worldwide. Its effectiveness, however, has 641 been questioned because studies conducted in Australia found that cleaning practices 642 stimulated fouling (Floerl 2002; Floerl et al. 2005). The potential for stimulating fouling is 643 further supported by the intermediate disturbance hypothesis (Grime 1973; Horn 1975; Connell 1978) that states recolonization may be more rapid following moderate disturbance such as 644 hull cleaning. We, however, found that the CPDA's cleaning practices did not stimulate the 645 646 recruitment of fouling organisms. The disparity among the studies likely is due to fundamental 647 differences in the practices employed, including the intervals between cleanings and the types 648 of tools used. Floerl (2002) allowed plates to accumulate fouling growth for seven months 649 before they were cleaned for the first time. In contrast, we cleaned experimental plates much 650 more frequently as per CPDA recommendations for the warm season in Southern California 651 (Johnson and Gonzalez 2004): every three weeks for plates coated with copper-based 652 antifouling paints and every two weeks for plates coated with nontoxic coatings. Floerl (2002) 653 also cleaned plates with a more abrasive tool, a paint scraper, whereas we cleaned the plate 654 surfaces with 3M[™] pads (soft- and medium-grade).

655

Longer cleaning intervals, like those used in the Australian studies, can increase the suitability of the surface for recruitment of fouling organisms. Fouling organisms are able to grow and some taxa become tougher or harder in texture as they mature. As a result, a more aggressive tool and greater effort are required to remove them, increasing the likelihood of scratching and/or chipping the protective hull coating. In addition, total removal of older, more developed organisms is more difficult and fragments of fouling organisms may be left attached to the surface. Consequently, there is an increase in the rugosity of the coating's surface, a

663 characteristic that many organisms prefer when searching for a place to settle (Crisp and 664 Barnes 1954; Petraitis 1990). Also, remnants of the fouling organisms could create a chemical 665 signal, attracting propagules to settle (Burke 1986; Pawlik 1992; Bryan et al. 1997, 1998). In 666 fact, Floerl (2002) found that prospective recruits to scraped plates were strongly influenced by 667 the types of fouling species that were on the plates prior to scraping. While we noticed very 668 small scratches on some of our experimental plates where small calcareous growth had been 669 removed, there were no noticeable deep scratches or fragments of organisms. In contrast, 670 Floerl and colleagues (2005) deemed sterilization was necessary to remove all traces of the 671 fouling assemblage to reduce subsequent fouling. These factors, at least in part, likely explain 672 the finding that hull cleaning stimulated fouling as reported in the Australian research. Our 673 results illustrate that the use of hull cleaning BMPs similar to those used in California can avoid 674 stimulated fouling. Other studies support our findings and the use of frequent and gentle hull 675 cleaning (Bergman and Ziegler 2018; Hunsucker et al. 2018, 2019).

676

677 Shorter cleaning intervals have the added benefit of not allowing fouling organisms to grow and 678 mature. As a result, the fouling organisms typically will be small and readily damaged when 679 cleaning occurs, likely not surviving the process. They also will have less time to develop, 680 reducing the likelihood that they will reach maturity. This is beneficial for two reasons. First, if 681 they are mature they can serve as a source of larvae that could potentially reseed boats and slips in the area, thereby hindering fouling management. Second, boats leaving the harbor with 682 683 mature fouling organisms represent a higher risk of transporting AIS to other areas with 684 suitable environmental conditions for the species.

685

686 Concerns have been raised about in-water hull cleaning as organisms removed during cleaning 687 activities are not typically contained and disposed on land (CDFW 2008). Instead the removed 688 material is allowed to sink to the bottom of the harbor. This practice could pose ecological risks 689 when a boat is cleaned at the home port after having visited another area where AIS may have 690 attached to the hull and been transported back to the home port. Some of this risk could be 691 avoided if boats are cleaned at the visiting port before returning to home port. In-water

692 cleaning of sedentary resident boats in their home port likely poses less ecological concern as 693 the attached fouling organisms already occur in the harbor. Nonetheless, dislodging adult 694 fouling organisms without lethal damage could allow these species to persist and continue to 695 reproduce on the harbor bottom, hindering biofouling management and potentially increasing 696 the risk of spreading AIS. Evaluating the survivorship of removed fouling organisms of different 697 taxa, ages and of those sinking to the bottom of the harbor would help determine whether this concern is warranted. If survivorship of removed fouling organisms is documented, then 698 699 research will be needed to develop practical, cost-effective collection technologies.

700

701 For boaters, durability of hull coatings is an important factor when considering hull cleaning 702 frequency. The primary benefit of slick coatings for recreational boat owners is ease of cleaning, 703 not hardness (aka durability). In contrast, nontoxic epoxy and ceramic-epoxy coatings neither 704 prevent nor reduce the strength of fouling organisms' attachment. Instead, they offer the 705 benefit of durability for boats whose hulls must be cleaned often (Lewis 2009). Watermann 706 (1999) discusses applying a hard, smooth anticorrosive system and maintaining it for several 707 years with regular underwater hull cleaning. Johnson and Gonzalez (2004) conducted a field 708 demonstration of frequently cleaned, nontoxic coatings on recreational boats in San Diego Bay 709 and follow-up surveys found that the tested epoxy coating lasted eight years and the ceramic-710 epoxy coating lasted over five years. In contrast, copper-based antifouling paints are replaced 711 every two to three years on recreational boats in that location (Carson et al. 2009). It may be 712 that more frequent cleanings using less abrasive tools (i.e., California-based hull cleaning 713 practices) could help extend the life of all coatings; a topic requiring further study.

- 714
- 715 [B]Cultural Tactics

Cultural tactics include practices that prevent or delay pest outbreaks, such as choosing sites that do not favor the pest, scheduling management tactics, and increasing efficacy by removing sources of the pest (FAO 2016; Flint 2012; Dafforn 2017). For hull fouling-control, these include practices associated with maintenance, like renewing hull coatings, scheduling hull cleaning, and removing sources of pests from dock floats. 721

[C] *Timing maintenance practices.*—As generally known, and further illustrated in our study, toxic hull coatings, such as copper-based antifouling paint, are most effective following initial application (< 6 months). Given this short time interval, application will be most effective at reducing hull fouling if applied just before peak recruitment when fouling organisms' larvae are most abundant and likely to settle on and attach to hard surfaces. Applying fresh toxic coatings to boat hulls at this time should greatly reduce fouling and the risk of spreading AIS at least for a few months.

729

Hull cleaning efficacy can be increased through careful planning of cleaning frequency and 730 731 timing based on: 1) Type and age of hull coating, 2) Time of year, 3) Harbor location and 4) Slip 732 location and conditions. Our results support the use of different hull cleaning frequencies for 733 toxic copper-based antifouling paints versus nontoxic hull coatings. Boats with copper-based 734 antifouling paint should be cleaned within the first 6 months after the toxic paint has been 735 applied, with more frequent cleaning as the paint ages and fouling accumulates more readily. In 736 comparison, nontoxic coatings require cleaning shortly after application and submersion of the 737 boat, and frequently from that time forward. Epoxy and slick coatings also may require more 738 frequent cleaning if certain taxa (Watersipora subatra, Hydroides spp.) are abundant where the 739 boat is kept.

740

741 Hull cleaning frequencies will be more efficient if they are adapted to seasonal variation in 742 recruitment of fouling organisms within a biogeographic area. Our earlier field demonstration 743 on boats in San Diego Bay (Johnson and Gonzalez 2004) and results presented here and 744 elsewhere (e.g., Underwood and Anderson 1994; Bullard et al. 2013) illustrate the high degree 745 to which fouling accumulation varies seasonally, supporting the use of different cleaning 746 frequencies throughout the year. When recruitment is low, the frequency of hull cleaning 747 activities could be reduced. In contrast, when recruitment of fouling organisms is high, frequent 748 cleanings would be most beneficial. The hull cleaning schedule could also be adjusted to 749 coincide with AIS recruitment patterns, especially those species with limited (1-3 months)

750 recruitment periods (e.g., F. implexa, B. neritina, Ciona spp.). Further, under California BMPs, 751 cleaning frequency is typically adjusted according to the coastal area where the boat is kept 752 (Johnson and Fernandez 2011; Johnson et al. 2012). Our findings support this adaptive 753 approach based on biogeography. Species in temperate regions are known to reach 754 reproductive maturity sooner and reproduce more often in warmer waters (Sastry 1963; Dugan 755 et al. 1991). Thus, more frequent hull cleaning is needed in temperate areas with warmer 756 water. This was evident during our study; experimental plates at the northern harbor were less 757 fouled and thus could have been cleaned less frequently than prescribed by the CPDA BMPs for 758 warmer southern waters.

759

760 On a finer spatial scale, slip location and associated conditions within a harbor may also need to 761 be considered when determining cleaning frequencies, particularly if AIS are present. For 762 example, the strong, negative response of *Ciona* spp. recruitment to enhanced flow found in a 763 related field experiment supports the hypothesis that water motion, and thus location in the 764 harbor, can influence distribution and abundance of this taxon (Santschi 2012). Similarly, 765 published and unpublished observations on W. subatra support the potential importance of 766 established colonies and water motion in influencing recruitment and early growth of this 767 bryozoan. W. subatra produces larvae with a very short planktonic life (24 hours or less) and 768 thus has limited dispersal ability. Page et al. (2006, 2019) and Simons et al. (2016) found that 769 this bryozoan recruited to settling plates deployed at offshore oil platforms with existing 770 colonies, but not to plates on platforms without these colonies. Our contrasting results on the 771 importance of environmental variables for recruitment and growth of W. subatra at our two 772 study locations may be related to differences in the range or magnitude of variation in these 773 variables between the different sized harbors, suggesting additional study of these responses is 774 needed.

775

The influence of environmental factors on recruitment of fouling organisms signifies that boats
kept in different locations within the same harbor may require different hull cleaning schedules
to control biofouling and limit AIS transport. Boats kept in slips far from the mouth of the

779 harbor where water flow typically is restricted may need to be cleaned more often when non-780 native invasive tunicates (e.g., Ciona spp.) are recruiting. Similarly, hulls of boats kept near the 781 mouth where flow is higher (or where the docks have higher cover of conspecifics) may need to 782 be cleaned on a schedule that is based on recruitment of the non-native bryozoan W. subatra. 783 Identifying areas within harbors where AIS and other species of concern to boaters are 784 persistent will help inform hull cleaning best management practices.

785

786 Light conditions within a slip may influence hull cleaning frequency. Light is required for algae 787 to grow and this was the primary fouling taxa occurring on the front of the plates, with 788 invertebrates dominating the back of the plates. These results are consistent with published 789 studies that found a dramatic effect of algal cover on invertebrate recruitment (Coyer et al. 790 1993; Raimondi and Morse 2000). However, the lower recruitment of invertebrates to the front 791 of the plates could also be related to a preference of some settling invertebrates for shaded 792 surfaces (Miller and Etter 2008). Regardless of the mechanism, boats kept in shaded areas may 793 experience higher recruitment of invertebrates, many of which are AIS, and consequently need 794 more frequent hull cleaning to reduce damage to hull coatings and the risk of transport of non-795 native species.

796

797 [C]Removal of biofouling source on docks.-Development of a system-wide control program 798 should include tactics that target harbor infrastructure. Fouling organisms attached to dock 799 floats, pier pilings and other structures provide a source of larvae that can re-infest cleaned 800 boat hulls. Knowing which species are present on these structures can help identify 'hot spots' 801 locations where species of concern, including non-native species and other fouling species 802 that are difficult to remove or cause damage when removed from boat hulls – occur. If hot 803 spots are found, harbor managers can concentrate removal efforts to reduce larval production 804 while minimizing the need to clean infrastructure frequently throughout the harbor. 805

806 Our investigation of dock floats indicated that only a small amount of this space was occupied 807 by fouling organisms other than algae. It is likely, however, that invertebrate fouling species

808 were present and more abundant on nearby surfaces of the docks and pilings where we were 809 not able to photograph or sample. Light exposure declines on the undersides of docks and with 810 water depths on the pilings, providing shaded surfaces where a higher proportion of fouling 811 invertebrates may be present. For this reason, surveying the undersides of docks and shaded 812 depths of pilings could be used to identify hot spots for specific fouling species, and allow for 813 targeted removal of these organisms. This approach could increase the efficiency of efforts to 814 reduce populations of fouling organisms in a harbor.

815

816 To implement this potentially useful tactic, cost-effective methods are needed for removing 817 fouling organisms from docks and pilings. Frequent dock scraping may be an option at smaller 818 harbors, but it is too labor intensive to be feasible in many areas. As noted earlier, research also 819 is needed to determine whether organisms scraped from hulls and docks into the water survive 820 and continue to reproduce in the harbor. If so, systems to remove and dispose fouling 821 organisms will need to be considered. Biological control agents that consume different stages 822 of fouling organisms are being evaluated and show some promise for controlling specific 823 species of concern (Culver et al. this issue; Culver et al. unpublished data) and fouling 824 communities as a whole (Atalah et al. 2014, 2016). No matter which tactic is used to remove 825 fouling, efforts focused at hot spots within harbors will help minimize costs. Ideally, removals from docks should also coincide with recruitment periods for native species to help minimize 826 827 the colonization of the newly cleaned open space by non-native taxa, particularly AIS.

828

829 IPM Framework for Hull Fouling Control

A summary of our hull fouling control framework is presented in Figure 15. It is based upon an IPM pyramid designed for the built environment (Underwood and López-Uribe 2019). Our pyramid applies basic principles of IPM, including the use of multiple tactics (represented by the tiers) that target all life stages of the pest and using more benign methods when possible. To be effective, these tactics should be used in combination as companion methods. The framework offers guidance to boaters for designing a fouling control strategy with tactics that address biofouling dynamics and factors associated with the boat and its use. A few additional tactics exist and new ones may be developed, all of which should be considered and incorporated intoan IPM strategy as necessary (Culver and Johnson 2012).

839

840 IPM strategies seek to limit the use of toxic chemicals by applying them only when needed and 841 in a way that minimizes their impacts on people and the environment (Flint 2012). Thus, they 842 appear at the top of the pyramid. Although toxic copper-based antifouling paints are 843 detrimental to water quality, their use will likely continue worldwide because they effectively 844 inhibit fouling of many species for at least six months. Considering water quality impacts and 845 the growing evidence for copper tolerance by fouling taxa, an IPM strategy could require a 846 reduced use of copper-based paints in areas where they have not already been prohibited. 847 Specifically, toxic hull coatings could be restricted to use only on boats that frequently travel 848 long distances. These boats represent a higher risk for transporting and spreading AIS to new 849 locations. If they are frequently out of port, such boats also represent a lower risk for 850 contributing to copper pollution in marinas. An important and notable exception is boats that 851 travel short distances to offshore islands, as islands are especially vulnerable to invasions 852 (Brockie et al. 1988; Reaser et al. 2007). Further, toxic antifouling paint could be applied only to 853 areas on boats that are critical for boat operations and difficult to clean manually (e.g., water 854 intakes, housings for outdrive units). Scheduling toxic paint application (a cultural tactic) just prior to the season when many fouling organisms recruit will also help maximize the 855 856 effectiveness of this strategy. In addition boats with toxic antifouling paint could be strategically 857 located (another cultural tactic) in slips with high water circulation so that copper leached from 858 coatings is less likely to accumulate in the harbor.

859

Avoiding the use of toxic antifouling paint for boats that travel infrequently or only short distances will further reduce impacts to water quality. These boats stay in the slip for extended periods and would be a source of leached toxins if toxic antifouling paint were applied. When considering the many available types of hull coatings, boaters will benefit by knowing whether a specific coating is more or less attractive to AIS or other species of concern. Importantly, while use of nontoxic hull coatings may be beneficial for water quality, when used alone they

represent a substantial risk for transporting AIS via boats even when newly applied. As
previously noted, many of these AIS can form dense aggregations and are difficult to remove
from boat hulls. This also is the case for boats with antifouling paints that have been
submerged for longer periods of time. These results reinforce the need to employ several
tactics that work together as companion methods to control hull fouling and the spread of nonnative species.

872

873 Companion fouling-control tactics are expected to become more important as the use of 874 nontoxic and less-toxic hull coatings increases in response to growing regulation of copper 875 antifouling paints. While tactics such as boat lifts and slip liners (with or without chlorine) are 876 an effective option, they are expensive, require maintenance and are not permitted at certain 877 harbors (Johnson and Fernandez 2011). This means that mechanical hull cleaning will remain an 878 important component of a hull fouling IPM strategy. Because the cost of land-based hull 879 cleaning, which requires lifting the boat out of the water and transporting it to a boat repair 880 yard, is considerably more expensive (Johnson and Fernandez 2011), in-water hull cleaning is 881 anticipated to remain the most common companion practice for boats kept in coastal harbors. 882 The CPDA recommended BMPs tested here, which require frequent cleanings using less 883 abrasive cleaning tools and effort, are beneficial for minimizing damage to hull coatings and 884 reducing spread of AIS. The benefits of these 'grooming' practices (frequent and gentle hull 885 cleaning) are also being reported for ships (Hunsucker et al. 2018, 2019).

886

887 As with chemical tactics, the efficacy of physical tactics can be enhanced through combination 888 with cultural tactics. Adjusting the frequency and timing of hull cleaning to recruitment patterns 889 of fouling organisms will enable boaters to better manage biofouling while also reducing 890 potential transport of AIS. For example, in temperate regions or ports with species of particular 891 concern, hull cleaning frequency may be increased during periods of intense fouling. In waters 892 where less fouling occurs in general, slip locations and conditions (particularly water flow, 893 shading and presence of conspecifics) may reveal areas within a harbor where more frequent 894 hull cleaning will be beneficial. For boats with nontoxic coatings or older antifouling paint,

frequent cleanings will be necessary. More generally, cleaning the hull just prior to leaving a port, especially if traveling far or to islands, is an effective cultural tactic for reducing the risk of transporting AIS and removing accumulated fouling (Culver and Johnson 2012). Cleaning harbor docks and other infrastructure is also an important cultural tactic to consider for system-wide hull fouling control. Integrating these tactics into fouling control strategies can address some of the complexities associated with fouling organism recruitment and the diversity of boating activities.

902

903 [B]Adoption of IPM for Boats

904 Application of an IPM approach for hull fouling control has only just begun. Discussions were 905 initiated in response to realized and anticipated regulatory changes regarding copper-based 906 antifouling paint and the need for hull fouling control methods that also considered risks 907 associated with AIS transport. Beforehand, water quality and AIS transport had not been 908 considered together. Previously developed measures often were beneficial for addressing only 909 one issue, while being detrimental to the other. Although we have not determined whether the 910 current IPM framework is being adopted, some marinas are taking steps that align with our 911 framework components. For example, as of 2015, the hull coatings on 41 boats (1.8% of boats 912 in the basin) had been converted to nonbiocidal coatings in response to a grant program in San 913 Diego, California (SDUPD 2015). Additional steps, including the requirement for in-water hull 914 cleaners to obtain a permit and follow the industry-recognized best management practices 915 (SDUPD 2012) that were a topic of our research, have been implemented. Overall, copper 916 loading has been reduced by an estimated 40.4% of the baseline (AFW 2016). It is anticipated 917 that IPM for hull fouling control will receive more attention as compliance schedules proceed 918 and more boaters switch to nontoxic coatings that require increased use of other fouling 919 control tactics.

We also expect that adoption of this integrated approach will increase as more boaters and key
community leaders learn and share the concept within the boating community (Rogers 2003).
Johnson and Fernandez (2011) found that boating-industry customer awareness of nontoxic
hull coatings significantly and positively influenced the use of these hull coatings. A majority

924 (76-100%) of participants in our educational workshops indicated that they intended to discuss 925 the various tactics and IPM framework with others, with a small percentage (12-20%) already 926 doing so. These results suggest that education may enhance dissemination of knowledge about 927 IPM strategies for hull fouling control in the boating community. This could increase the 928 likelihood that IPM will be adopted when regulations require boat owners to reduce use of 929 copper antifouling paints and/or for boat owners seeking a more environmentally friendly 930 fouling control strategy. Follow-up surveys of participants would provide further insight into 931 actual adoption of the various tactics.

932



934 Use of IPM to control biofouling on boat hulls is a new concept that requires evaluation and 935 modification as scientific research continues, additional tactics become available, and more 936 boat owners apply this approach. As a first step, we concentrated on factors influencing fouling 937 for boats that rarely move; the case for half of all boaters in California. Additional research on 938 the influence of boat use frequency and cruising speed on biofouling is critically needed to 939 make an IPM strategy more broadly applicable. Nonetheless, an IPM framework as outlined 940 here (Fig. 15) can provide a means for simultaneously addressing issues of water quality and AIS 941 transport on boat hulls, while controlling biofouling. Adaptive in nature, it is not a "one size fits 942 all" approach; it needs to be tailored to local conditions and individual boating patterns. As 943 such, our IPM framework can be applied in areas where copper-based antifouling paints will 944 continue to be used, as well as areas where the use of these toxic paints has been or will be 945 restricted. Overall, this framework uses a sound and well-proven approach for pest 946 management to facilitate an adaptive approach for biofouling control that balances the need 947 for efficient boat operations while minimizing impacts to ecosystem health.

948

949 [A]Acknowledgements

950 We gratefully acknowledge our project sponsors (listed below) and the key cooperators at the

- 951 Waterfront Department, City of Santa Barbara, Half Moon Anchorage, Kona Kai Marina,
- 952 Southwestern Yacht Club, and Shelter Island Boat Yard. We thank the many people that

953 provided advice and assistance with the research associated with this work including Scott 954 Parker, Gary Tanizaki and other staff and students at the University of California Santa Barbara, 955 and University of California Cooperative Extension, San Diego County. We are grateful to many 956 taxonomists who provided identification of voucher specimens at the Moss Landing Marine 957 Laboratories, Los Angeles County Museum of Natural History, Oregon State University, Santa 958 Barbara Museum of Natural History and University of California Santa Barbara. Thanks also are 959 extended to Phil Phillips and Cheryl Wilen, University of California Cooperative Extension, for 960 their review of related materials, and to anonymous reviewers for their helpful comments that 961 improved the manuscript. Figure 15 was adapted from Pennsylvania State Extension's pyramid 962 illustration and further refined by us and designer Benjamin Paul Dianna, University of 963 California Cooperative Extension, San Diego and Katherine Leitzell and Caitlin Coomber, 964 California Sea Grant.

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This work was supported through Agreement Number 07-106-111 with the California
Department of Boating and Waterways, as well as by NOAA Grants Nos. NA10OAR4170060,
NA08OAR4170669 and NA04OAR4170038, California Sea Grant Project No. A/EA-1 through
NOAA's National Sea Grant College Program, U.S. Dept. of Commerce; University of California
Agriculture and Natural Resources; University of California Cooperative Extension; California
Resources Agency; and Counties of San Diego, Santa Barbara and Ventura.

The statements, findings and conclusions in this manuscript are those of the authors and not necessarily those of the California State Parks Division of Boating and Waterways, nor of the other sponsors. The mention of commercial products, their source, or their use in connection with material reported herein is not to be construed as actual or implied endorsement of such products.

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Table 1. Design information for the field studies and experiments conducted for this study. Single asterisk (*) denotes that the same onemonth gel treatment plates were evaluated for two of the experiments. Double asterisk (**) denotes that the front and back plate surfaces were combined for the analyses. Triple asterisk (***) denotes that only the front of the plates were analyzed. Four replicate frames were deployed at each location.

1389

Study	tudy sites	Frame size	Treatments	Coatings	Fouling	Number of	Duration	Time
	locations)	(instruments)			accumulation	plates	(months)	frame
	5				time intervals	(surfaces)		
Hull Coating	SBH (4)	1m x 1m	4*	4 (all)	1 month	1340	12	April 2008-
\geq	SIYB (3)					(2680)		March 2009
Aging copper-	SIYB (2)	1m x 0.5m	3	1 (copper)	3, 6, 12	24	12	July 2008-
based antifouling					month	(48**)		June 2009
paint								
±								
Hull cleaning	SBH (1)	1m x 1.5m	3	3	1 month	108	4	June 2008-
	SIYB (2)			(all, less gel)		(108***)		Sept 2008
	1							
Time of year	SBH (4)	1m x 1m	1*	1 (gel)	1 month	419	15	April 2008-
	SIYB (3)					(838)		June 2009
	Study Study Hull Coating Aging copper- based antifouling paint Hull cleaning Time of year	StudyStudy sites (locations)Hull CoatingSBH (4) SIYB (3)Aging copper- based antifouling paintSIYB (2) SIYB (2)Hull cleaningSBH (1) SIYB (2)Time of yearSBH (4) SIYB (3)	Study Frame size (instruments) Hull Coating SBH (4) (instruments) Hull Coating SBH (4) (instruments) Aging copper SIYB (3) Aging copper SIYB (2) (instruments) Hull cleaning SBH (1) (instruments) Hull cleaning SBH (1) (instruments) Time of year SBH (4) (instruments) SIYB (2) Im x 1.5m (instruments) SIYB (2) Im x 1.5m (instruments)	Study Study sites Frame size Treatments Hull Coating SBH (4) 1m x 1m 4* Aging copper SIYB (3) 1m x 0.5m 3 based antifouling SBH (1) 1m x 1.5m 3 Hull cleaning SBH (1) 1m x 1.5m 3 Time of year SBH (4) 1m x 1m 1* SIYB (3) 1m x 1m 1* SIYB (3) 1m x 1m 1*	Study Study sites Frame size (instruments) Treatments Coatings Hull Coating SBH (4) (instruments) 1m x 1m 4* 4 (all) Hull Coating SIYB (3) 1m x 0.5m 3 1 (copper) based antifouling paint SBH (1) 1m x 1.5m 3 3 (all, less gel) Hull cleaning SBH (1) 1m x 1m 1* 1 (gel) Time of year SBH (4) (3) 1m x 1m 1* 1 (gel)	StudyFrame size (instruments)TreatmentsCoatingsFouling accumulation time intervalsHull CoatingSBH (4) SIYB (3)1m x 1m4*4 (all)1 monthAging copper based antifoulingSIYB (2) SIYB (2)1m x 0.5m31 (copper)3, 6, 12 monthHull cleaningSBH (1) SIYB (2)1m x 1.5m331 monthHull cleaningSBH (1) SIYB (2)1m x 1.5m331 monthFrame size based antifoulingSBH (1) SIYB (2)1m x 1.5m331 monthHull cleaningSBH (1) SIYB (2)1m x 1.5m331 monthFrame size (all, less gel)SBH (4) SIYB (3)1m x 1m1*1 (gel)1 month	StudyStudy sites (instruments)Frame size (instruments)TreatmentsCoatingsFouling accumulation time intervalsNumber of plates (surfaces)Hull CoatingSBH (4) SIYB (3)1m x 1m4*4 (all)1 month1340 (2680)Aging copper based antifoulingSIYB (2) SIYB (2)1m x 0.5m31 (copper)3, 6, 12 month24 (48**)Hull cleaningSBH (1) SIYB (2)1m x 1.5m33 (all, less gel)1 month108 (108***)Time of yearSBH (4) SIYB (3)1m x 1m1* (gel)1 month419 (838)	StudyFrame size (instruments)TreatmentsCoatings accumulation time intervalsNumber of plates (surfaces)Duration (months)Hull CoatingSBH (4) SIYB (3)1m x 1m4*4 (all)1 month1340 (2680)12 (2680)Aging copper based antifoulingSIYB (2)1m x 0.5m31 (copper)3, 6, 12 (all, less gel)24 (108***)12 (2680)Hull cleaning SIYB (2)1m x 1.5m33 (all, less gel)1 month108 (108***)4 (108***)Time of yearSBH (4) SIYB (3)1m x 1m1*1 (gel)1 month419 (838)15 (838)

1409	Location and	SBH (4)	1m x 1m	n/a	n/a	1 month	n/a	12	April 2008-
1410	environmental	SIYB (3)	(SLOD™/						March 2009
1411	factors		(OBO™)						
	\triangleleft	1							

1408

1412Table A.1. Species recruiting to plates with nontoxic coatings submerged for one month at both the1413northern (Santa Barbara Harbor) and southern (Shelter Island Yacht Basin) harbors. Origin: C,1414cryptogenic; N, native; NN, non-native; Unr, unresolved, UnID, unidentified. Coating Type: E, epoxy; S,1415slick; G, gel base. "-", species absent. "x", species present. Single asterisk (*) denotes very rare species1416that were found on only one plate at one time at a site. Double asterisk (**) denotes rare species that1417were found on one to five plates.

1418						
1419				Coa	ting ty	pe
1420	Phyla	Species	Origin	Ε	S	G
1421		0				
1422	Algae					
1423	Chlorophyta	Cladophora sp.	Unr	х	x	x
1424		Colpomenia sp.	Unr	х	x	x
1425	5	Ectocarpacea	Unr	х	x	x
1426	6	Enteromorpha sp.	Unr	х	x	х
1427		Ulva sp.	Unr	x**	X**	X**
1428	Rhodophyta	Rhodymenia pacifica	Ν	-	-	x*
1429		Antithamnion sp.	Unr	х	x	х
1430	Invertebrates					
1431	Annelida	Filograna implexa	NN	х	x	х
1432	C	Hydroides spp. complex				
1433		H. elegans, H. gracilis	NN/N	х	x	х
1434	_	Myxicola sp. A - Harris	Unr	x*	-	-
1435		Sabellid				
1436		(likely <i>Pseudopotamilla</i> sp.)	UnID	x*	-	-
1437		Spirorbid sp.	Unr	x	x	x
1438	Mollusca	Mytilus sp.	UnID	x*	-	-
1439	Chordata	Aplidium californicum	Ν	x	x	x
1440		Ascidia ceretodes	Ν	-	-	-
1441		Ascidia zara	NN	-	-	-
1442		Botrylloides diegensis	N	х	х	х

	Botrylloides violaceus	NN	х	х	х
	Botryllus schlosseri	NN	x	x	х
	Ciona spp.				
	C. intestinalis or C. savignyi	NN/NN	x	x	х
	Styela clava	NN	x	-	-
	Styela montereyensis	N	-	-	-
	Styela plicata	NN	x	x	х
	Diplosoma listerianum	NN	x	x	х
	Molgula sp. (most likely				
	M. ficus or M. verrucifera)	Unr	x**	x**	-
	Unidentified tunicates (n=3)	UnID	x	x	x**
Crustacea	Laticorophium baconi (tubes)	С	x	x	х
Bryozoa	Bugula californica	N	x	x	х
	Celleporaria brunnea	Ν	x	x	х
	Crisulipora occidentalis	Ν	x	x	х
	Thalamoporella californica	N	x	x	х
	Tubulipora sp.				
	(Either <i>T. tuba</i> or <i>T. pacifica</i>)	Ν	x	x	х
	Bugula neritina	NN	x	x	х
	Cryptosula pallasiana	NN	x	x	х
	Watersipora subatra	NN	x	x	х
	Bowerbankia sp.	Unr	x	х	х
	Membranipora sp.	Unr	x	x	х
Porifera	Unidentified sponges (n=2)	UnID	-	x**	x*
	Crustacea Bryozoa	Botrylloides violaceus Botryllus schlosseri Ciona spp. C. intestinalis or C. savignyi Styela clava Styela plicata Diplosoma listerianum Molgula sp. (most likely M. ficus or M. verrucifera) Unidentified tunicates (n=3) Unidentified tunicates (n=3) Bryozoa Bryozoa Crustacea Bugula neritina Cryptosula pallasiana Watersipora subatra Bowerbankia sp. Membranipora sp. Porifera	Botrylloides violaceusNNBotryllus schlosseriNNCiona spp.NN/NNC. intestinalis or C. savignyiNN/NNStyela clavaNNStyela plicataNNDiplosoma listerianumNNDiplosoma listerianumNNMolgula sp. (most likelyUnrM. ficus or M. verrucifera)UnlDCrustaceaBugula californicaNBryozoaCelleporaria brunneaNCrustaceaNNBryozoaCelleporaria brunneaNCrisulipora occidentalisNCrustaceaNBryozoaCelleporaria brunneaNCrisulipora sp.(Either T. tuba or T. pacifica)NBugula neritinaNNBugula neritinaNNBugula resiburacianaNNMottersipora subatraNNBowerbankia sp.UnrMembranipora sp.Unr	Botrylloides violaceusNNxBotryllus schlosseriNNxCiona spp.C. intestinalis or C. savignyiNN/NNxStyela clavaNNxStyela clavaNNxStyela plicataNNxDiplosoma listerianumNNxM. ficus or M. verrucifera)Unrx**M. ficus or M. verrucifera)UnlDxCrustaceaBugula californicaNxBryozoaCelleporaria brunneaNxCrustaceaKerisulipora occidentalisNxBryozoaCelleporaria brunneaNxCrustaceaNNxxBryozoaMalamoporella californicaNxMembranipora sp.(Either T. tuba or T. pacifica)NNxMembranipora sp.UnrxxBowerbankia sp.UnrxPoriferaUnidentified sponges (n=2)UnlD-	Botrylloides violaceus NN x x Botryllus schlosseri NN x x Ciona spp. C. intestinalis or C. savignyi NNN x x Styela clava NN x x x Styela plicata NN x x Diplosoma listerianum NN x x Molgula sp. (most likely N. x x M. ficus or M. verrucifera) Unir x** x** Bryozoa Bugula californica N x x Erustacea Bugula californica N x x Bryozoa Eugliora occidentalis N x x Bugula californica N x x Crustacea NN x x x Bugula californica N x x x Crustacea Bugula californica N x x Bugula californica N x x x Crustacea NN x x x Euglia nerit

1467

1468Table A.2. Species recruiting to plates coated with copper-based antifouling paint submerged for up to1469twelve months. The shortest submersion time (1 month) includes data from all locations at both1470harbors, with the longer submersion times (3, 6, 12 months) including data from two locations at the1471southern harbor (Shelter Island Yacht Basin). Origin: C, cryptogenic; N, native; NN, non-native; Unr,1472unresolved, UnID, unidentified. "-" species absent. "x", species present. Single asterisk (*) denotes very1473rare species that were found on only one plate at one time at a single site. Double asterisk (**) denotes

			Submersion time (month)			
Phyla 🔹	Species	Origin	1	3	6	12
Algae	2					
Chlorophyta	Cladophora sp.	Unr	х*			
	Colpomenia sp.	Unr			x*	
	Enteromorpha sp.	Unr	х			
	Green monofilament	UnID		x*		
Rhodophyta	Rhodymenia pacifica	Ν			x**	х
Invertebrates						
Annelida	Filograna implexa	NN		х	х	х
	Hydroides spp. complex					
	H. elegans, H. gracilis	NN/N	х	х	х	х
	Sabellid	Unr	х			
	Spirorbid sp.	Unr	х	x	х	х
Chordata	Aplidium californicum	Ν				х
	Botrylloides diegensis	Ν				x*
	Botrylloides violaceus	NN				x*
	Ciona sp.					
	C. intestinalis or C. savignyi	NN		x*		х
	Diplosoma listerianum	NN	х	x*		х
Crustacea	Laticorophium baconi					
	(tube mats)	С	х	х	x	х
Bryozoa	Bowerbankia sp.	Unr		х	x	х
	Bugula californica	Ν				х
	Bugula neritina	NN			х	х
	Celleporaria brunnea	N			x*	

1474 species that did not recruit directly to the plates. Highlighted (bold) species occupied the most space

1475 over time.

1476

1505		Crisulipora occidentalis	Ν		х*
1506		Cryptosula pallasiana	NN		x*
1507		Thalamoporella californica	Ν	x*	
1508		Watersipora subatra	NN	х	х
1509	Porifera	Sponge	UnID		x*

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(B) Shelter is and Yotht Basin, Sch Diego Bay



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us (A) Inter location (Half Moon Anchorage)





Non natives

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(A) Sente Berbaraherber

a Never Clashed a Glocher, Orice





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Janus IN N **----**





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