

1 Oceanographic and biological influences on recruitment of
2 benthic invertebrates to hard substrata on the Oregon shelf

3

4 Kirstin S. Meyer^{a,c*}, Yizhen Li^{b,d} and Craig M. Young^a

5

6 ^aOregon Institute of Marine Biology, 63466 Boat Basin Road, Charleston, OR 97420

7 ^bApplied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, 266 Woods
8 Hole Road, Woods Hole, MA 02543

9 ^cPresent address: Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole
10 Road, Woods Hole, MA 02543

11 ^dPresent address: CSS Inc. under contract to National Centers for Coastal Ocean Science,
12 NOAA, 1305 East West Highway, Silver Spring, MD 20910

13 *Corresponding author e-mail: kimeyer@alumni.nmu.edu

14

15 **Abstract**

16 The number of anthropogenic substrata in the ocean – structures like oil rigs and offshore
17 renewable energy generators – is increasing. These structures provide hard-bottom habitat in
18 areas previously dominated by sand or mud, so they have the potential to alter species
19 distributions or serve as “stepping-stones” between other hard-bottom habitats. It is thus
20 important to understand what factors influence the composition and abundance of benthic fauna
21 recruiting at these sites. We examined recruitment to hard substrata (fouling panels) deployed on
22 sand at various distances from a large rocky reef (~60 m isobath) on the southern Oregon coast

1 in 2014 – 2015. Recruitment was dominated by the acorn barnacle *Hesperibalanus hesperius*.
2 For the majority of the study period in 2014, an anti-cyclonic eddy was present near the
3 deployment sites. However, anomalously high recruitment of *H. hesperius* during August – early
4 October 2014 coincided with dissipation of the eddy, slower bottom currents, and a positive
5 convergence index, suggesting that *H. hesperius* larvae from the adjacent area may have been
6 accumulated and retained near our study sites. Other sessile species, including hydroids and
7 bryozoans, recruited to the fouling panels in low abundances, and most of these species have
8 long-range dispersal and fast growth. Mobile invertebrates observed on the fouling panels
9 included gastropods and nudibranchs, most of which also have long-range dispersal and fast
10 growth, and are predators as adults. Thus, a community with two trophic levels assembled on the
11 fouling panels in a relatively short time period (<12 weeks). None of the common hard-bottom
12 species from the adjacent rocky reef recruited to the panels, suggesting that there is a specialized
13 assemblage of species that can exploit hard-bottom habitats surrounded by sandy plains. Our
14 results raise many questions about the influences of dispersal and oceanographic conditions on
15 recruitment to hard substrata.

16

17 **Keywords**

18 Community assembly, rocky reef, barnacle, *Hesperibalanus hesperius*, bottom current,
19 convergence

20

21 **1. Introduction**

22 Most of the continental shelves are blanketed by soft sediments, so hard-bottom habitats
23 are often isolated and island-like (Wahl, 2009). These habitats include rocky reefs (Steimle and

1 Zetlin, 2000; Tuya et al., 2004), coral reefs (Bellwood and Hughes, 2001; Jones et al., 2009),
2 artificial reefs (Perkol-Finkel et al., 2006; Perkol-Finkel and Benayahu, 2005), anthropogenic
3 structures such as oil platforms (Bram et al., 2005; Page et al., 2008) and litter (Bergmann et al.,
4 2015).

5 Community assembly on hard substrata has been studied for artificial reefs in the tropics
6 (Perkol-Finkel et al., 2005; Perkol-Finkel and Benayahu, 2009, 2007), but relatively little is
7 known about how new hard-bottom communities develop at temperate latitudes. The increasing
8 numbers of anthropogenic substrata on continental shelves, such as offshore wind platforms and
9 wave-based energy generators (De Mesel et al., 2015; Krone et al., 2013; Miller et al., 2013),
10 could alter species distributions of hard-bottom fauna as they become fouled. Anthropogenic
11 substrata provide hard-bottom habitats where there was previously only sand or mud and could
12 serve as “stepping-stones” between natural reefs. The potential ecological impacts make it
13 important to understand how communities may develop on these substrata.

14 There are already plans for the installation of wave-based energy generators offshore of
15 Reedsport, Oregon, near our study sites (Elwood et al., 2010). These energy installations include
16 large anchors on the seafloor that could become fouled (Elwood et al., 2010; Scruggs and Jacob,
17 2009). Numerous subtidal rocky and biogenic reefs on the Oregon coast could serve as sources
18 of larvae, leading to the colonization of seafloor anchors by benthic invertebrates (Gunderson et
19 al., 2008; Pearcy et al., 1989; Posey et al., 1984).

20 Recruitment is influenced by larval supply, larval transport, settlement, and post-
21 settlement processes, and the interactions of these factors (Pineda et al., 2009). Post-settlement
22 mortality can be high in some species, decoupling the processes of settlement and growth to
23 adulthood (Hunt and Scheibling, 1997). Despite these limitations, studies on key species and on

1 meso- or local scales can increase our understanding of recruitment dynamics (Hadfield, 1986;
2 Pineda et al., 2009).

3 Larval dispersal of benthic invertebrates is often affected by coastal circulation patterns
4 and oceanographic conditions (Chiswell and Roemmich, 1998; Hutchings and Pearce, 1994;
5 Limouzy-Paris et al., 1997), with larvae becoming entrained by temporary or semi-permanent
6 eddies and being retained near shore (Chiswell and Booth, 1999; Lobel and Robinson, 1988).

7 The Oregon coast is well-known for baroclinic mesoscale eddies, which interact with the coastal
8 upwelling system through cross-shelf mass transport (Capet et al., 2008; Strub et al., 1991).

9 Therefore, we investigated how oceanographic conditions might influence recruitment of benthic
10 invertebrates on hard substrata.

11 We deployed artificial substrata (fouling panels) at five sites on the seafloor, near the 60
12 m isobath. Sites were located 0 – 9 km from a rocky reef south of Cape Arago, which is
13 inhabited by a diverse array of sponges, bryozoans, soft corals, and anemones, as well as
14 holothurians, crabs, and fish (Young et al., unpublished data).

15 We first describe the temporal and spatial patterns in recruitment of benthic invertebrates
16 on the hard substrata. We then describe on a population level how recruitment of the most
17 common species, the barnacle *Hesperibalanus hesperius*, correlated with changes in
18 oceanographic conditions. Finally, on a community level, we compare the identities and
19 functional traits of recruiting species to those present on the adjacent rocky reef, and discuss
20 what our results imply about community assembly in hard-bottom habitats.

21

22

23

1 2. Methods

2 Fouling panels (15 x 15 cm) were constructed from clear plexiglass (0.32 cm thick) and
3 scored on one side with sandpaper (100 grit) to provide a rugose texture suitable for settlement.
4 The resulting shallow scratches on the panels were 0.3 – 1 mm apart, on a comparable spatial
5 scale to the fine roughness elements that have been shown to increase barnacle recruitment in
6 previous studies (Hills and Thomason, 1998; Lemire and Bourget, 1996). Panels were attached to
7 cement blocks (38 x 38 x 20 cm) using stainless steel bolts (0.63 cm x 10 cm) embedded in the
8 cement – one bolt through the middle of the plate – and secured with a wingnut. Two panels
9 were deployed on each vertical side of each block, for a total of eight panels per block (Fig. 1). A
10 galvanized steel eye bolt was embedded in the top of each block and served as an attachment
11 point for a line and surface float.

12 Blocks were deployed in pairs at five locations along the southern Oregon coast (43° 17'
13 – 43° 21' N, 124° 24' – 124° 27' W, ~ 60 m depth) within and at various distances from the
14 rocky reef (0 – 9 km, Fig. 2). In 2014, blocks were recovered every 3 weeks using R/V *Pluteus*,
15 with some variation in the schedule due to weather. Half of the fouling panels on each block
16 were removed and replaced after 3 weeks, while the other half were left on the blocks for a 6-
17 week deployment. Fouling panels in 2014 were at sea for 21-51 days. In 2015, a combination of
18 weather and logistical difficulties thwarted the planned 3-week schedule, so blocks were
19 deployed and recovered together, spending 79 days on the seafloor (Table 1).

20 Following recovery, fouling panels were transported in containers of seawater aboard
21 R/V *Pluteus* and maintained in flow-through seawater tanks at the Oregon Institute of Marine
22 Biology (OIMB). All sessile invertebrate recruits present on the front (outward-facing) side of
23 the fouling panels were counted and identified. Specimens were photographed using a digital

1 camera (Canon) on a dissecting microscope (Olympus). For broken panels, the surface area was
2 estimated, and the number of sessile individuals present in that area was extrapolated to 225 cm².
3 Mobile invertebrates on the panels were also noted and counted if possible, though mobile
4 organisms often crawled and/or washed off of fouling panels into the surrounding tanks, making
5 accurate counts per plate impossible. We only report the total abundance on all plates for the
6 mobile invertebrates.

7 In order to characterize the interaction between oceanographic conditions and
8 recruitment, we calculated the convergence index and average current speed for surface and
9 near-bottom waters at the study sites during each deployment, using the data-assimilative
10 Hybrid-Coordinate Ocean Modeling (HYCOM, <https://hycom.org/>, Chassignet et al. 2007).
11 Comparisons between HYCOM surface elevation and AVISO (Archiving, Validation and
12 Interpretation of Satellite Oceanographic data) sea surface height suggests that HYCOM
13 represents the evolution of eddies during our observational period well (data not shown), and
14 thus can be used as a good approximation of ocean circulation conditions during the study
15 period. Recruitment was pooled for all sites within a deployment and standardized by the number
16 of days of deployment for a comparison with oceanographic conditions. We explored the
17 relationships between barnacle recruitment, the convergence index, and current speed using
18 Spearman correlations.

19

20 **3. Results**

21 The most common recruiting species on our fouling panels was the acorn barnacle
22 *Hesperibalanus hesperius*, accounting for 96.7% of all sessile individuals. Patterns in barnacle
23 recruitment are reported below. The second most common species was the hydrozoan *Clytia*

1 *hemisphaerica*, with 3.0% of recruiting individuals. This species had much higher recruitment at
2 site 4 during deployments A3 and B2, in July-August 2014, than at other sites or during other
3 deployments (Fig. 3).

4 Other recruits observed on the fouling panels in lesser proportions were the bryozoan
5 *Celleporella hyalina*, the anemone *Metridium senile*, a juvenile mussel and a spirorbid
6 polychaete that could not be further identified (Table 2). These sessile species showed no
7 patterns with regards to recruitment on panels deployed for different durations, with the possible
8 exception of *M. senile*, which was present in much higher abundance on panels deployed for 79
9 days than on panels deployed for shorter durations (Table 2).

10 A number of mobile species were observed on the fouling panels, including the
11 nudibranchs *Hermisenda crassicornis*, *Onchidoris bilamellata*, and *Pleurobranchaea*
12 *californica*, the whelk *Alia gausapata*, and the flatworm *Notocomplana* sp (Table 2). Each of
13 these species was observed on the front (outward-facing) side of the fouling panels, among the
14 barnacles. *Notocomplana* sp. and *O. bilamellata* both were present in higher abundances during
15 deployments C and D, in August – October 2014, compared to deployments earlier in that year.
16 *Alia gausapata* was much more abundant on panels recovered after 79 days than on panels
17 deployed for shorter durations (Table 2).

18 *Hesperibalanus hesperius* recruited in high densities to fouling panels at all sites except
19 site 5, located in the rocky reef (Fig. 4). Two barnacles were found on a single panel at site 5,
20 and the remaining panels had either one or no barnacles. There was a significant linear
21 correlation between the number of barnacles recruiting panel⁻¹ day⁻¹ and distance from the reef
22 (Spearman correlation, rho = 0.234, p = 0.001), with more barnacles recruiting at sites further

1 from the reef. Sites 4 and 3 had anomalously higher barnacle recruitment during deployments C
2 and D, in August – early October 2014 (Fig. 4).

3 Sea surface height in July 2014 showed two cold filaments encompassing an anti-
4 cyclonic eddy west of the substratum deployment sites (Fig. 5A). The eddy evolved to move
5 onshore in August and became entrained in the coastal region, forming an ideal circular shape in
6 September. In October, the eddy started to become smeared as it interacted with the coastal flow,
7 and water from the eddy no longer rotated anti-cyclonically but flowed offshore. In 2015, the
8 extent of eddy activity is less clear (Fig. 5A). However, in August, there was a pair of linked
9 gyres just south of the deployment sites.

10 Compared to surface currents, bottom currents during the deployments were generally
11 slow (1 – 6 cm/s). Despite some vertical shear, current velocities near bottom and at the surface
12 were in phase (Fig. 5B), suggesting the current is dominated by a barotropic mode. To better
13 quantify the relationships between current patterns and barnacle recruitment, we computed the
14 convergence index for each deployment. The convergence index was negative for every
15 deployment except deployment D, when anomalously high recruitment was observed, in August
16 – early October 2014 (Fig. 6).

17 There was a significant positive correlation between barnacle recruitment and the
18 convergence index for near-bottom waters (Spearman correlation, $\rho = 0.78$, $p = 0.02$) (Fig.
19 6C). Correlations between barnacle recruitment and the surface convergence index, surface
20 current, and near-bottom current velocity were non-significant but show suggestive trends ($p >$
21 0.05 , Fig. 6A, B, D). The highest recruitment occurred during deployments with decelerated
22 current velocity and a positive convergence index (Fig. 6).

23

1 4. Discussion

2 4.1 The barnacle *Hesperibalanus hesperius*

3 The acorn barnacle *Hesperibalanus hesperius* was by far the most abundant recruit on the
4 fouling panels in this study. Acorn barnacles are typically the first recruits on subtidal substrata
5 (García and Moreno, 1998; Hudon et al., 1983; Osman, 1977) and are well-documented pioneer
6 species (Berntsson et al., 2000; Berntsson and Jonsson, 2003; Keough and Raimondi, 1996).
7 *Hesperibalanus hesperius* has long-duration planktotrophic larvae (Barnes and Barnes, 1959)
8 and grows quickly after settlement but lives for only 6-7 months (Ovsyannikova and Levin,
9 1982). It thus can be characterized as a pioneer species with long-range dispersal, fast growth,
10 and early sexual maturity. The dominance of *H. hesperius* on the fouling panels in this study is in
11 line with previous studies on subtidal succession, where acorn barnacles are typically the first
12 abundant species on fouling panels (Chalmer, 1982; Osman, 1977). However, *H. hesperius* has
13 seldom been documented in Oregon (Carlton, 2007; Shanks, 2001), and to our knowledge, this
14 study represents the first report of dense recruitment of this species in the eastern Pacific. Larvae
15 of *H. hesperius* have been observed in Friday Harbor, Washington (Barnes and Barnes, 1959)
16 and adults appear in fossil records (Boessenecker, 2013; Zullo and Marinovich, 1990), but most
17 studies on *H. hesperius* have been conducted in Peter the Great Bay, Russia (Kulikova and
18 Omelyanenko, 2005; Ovsyannikova and Levin, 1982; Silina, 2002; Zhukova, 2000). Very little is
19 known about the modern distribution, reproduction, and ecology of *H. hesperius* in the eastern
20 Pacific.

21 It is unclear why only *Hesperibalanus hesperius* recruited to settlement plates in this
22 study, rather than any other balanoid barnacle. Other barnacle species present in subtidal habitats
23 on the Oregon coast include *Balanus crenatus*, *B. nubilus*, *B. trigonus*, and the introduced

1 *Amphibalanus amphitrite* (Carlton, 2007). *Balanus nubilus* is present on the rocky reef adjacent
2 to our study sites (Meyer, unpublished data). These species each have long-duration (weeks)
3 planktotrophic larvae (Herz, 1933; Lee and Kim, 1990; Shanks, 2001), so they would likely be
4 able to reach the isolated settlement plates in this study. *H. hesperius* is most commonly
5 observed on crab carapaces and mollusk shells (Carlton, 2007; Ovsyannikova and Levin, 1982),
6 so one potential explanation is that it is outcompeted by other balanoid species on natural rock
7 substrata and is therefore adapted to life on alternative or sub-optimal isolated substrata. The
8 sandy shelf surrounding our study sites support a major fishery for Dungeness crabs, which may
9 constitute the source population for *H. hesperius* recruitment.

10

11 4.2 Influence of oceanographic conditions on recruitment of *Hesperibalanus hesperius*

12 Anomalously high recruitment of *Hesperibalanus hesperius* was observed during
13 deployments C and D, in August – early October 2014 (Fig. 3). During this time period, bottom
14 current was decelerated and the convergence index for deployment D was the only positive value
15 during the deployments. A negative convergence index (=divergence) indicates that particulate
16 matter was being carried away from the study area, while a positive convergence index suggests
17 circulation favored retention and aggregation of material, including larvae. The mesoscale eddy
18 in September 2014 (Fig. 4) likely played an important role in retention of larvae near the
19 substrata. Larval retention can lead to high recruitment by holding larvae in one area during the
20 competency period, allowing them to recruit to substrata there, as suggested by other relevant
21 studies (Chiswell and Booth, 1999; Chiswell and Roemmich, 1998; Lobel and Robinson, 1988).

22 Higher recruitment of *Hesperibalanus hesperius* during deployments C and D also
23 coincided with slower bottom current. High current velocities can sweep larvae off of a

1 substratum, rendering them unable to attach and metamorphose (Koehl, 2007). However, the
2 bottom current speeds calculated from the HYCOM model in this study are 1 – 6 cm/s, a range
3 that has been used to represent slow current conditions conducive to larval settlement in previous
4 laboratory flume studies (Crimaldi et al., 2002; Koehl et al., 2013). Larvae are not likely to be
5 swept off a substratum at the velocities calculated in this study; however, the negative
6 convergence index indicates that during most of our deployments, larvae were being carried
7 away from our study area.

8 Overall, slower current speed along with a positive horizontal convergence rate coincided
9 with elevated recruitment, largely because more larvae were delivered to the fouling panels. Our
10 results indicate that regional oceanographic conditions had a stronger influence on *H. hesperius*
11 recruitment than the presence of the rocky reef. The relationships between *H. hesperius*
12 recruitment and oceanographic conditions in this study are correlative and non-experimental, and
13 further particle tracking using high-resolution numerical models, laboratory experimentation, and
14 field studies will be necessary to more completely understand how mesoscale circulation affects
15 recruitment.

16

17 4.3 Other sessile recruits on fouling panels

18 A small number of species besides *Hesperibalanus hesperius* recruited to fouling panels
19 in this study. These species have many similar life-history characteristics to *H. hesperius* and
20 could be characterized as pioneer species. For example, the bryozoan *Celleporella hyalina* has a
21 cosmopolitan distribution (Hoare et al., 2001), fast growth, short life span, and early sexual
22 maturity (Cancino and Hughes, 1987). Larvae of *C. hyalina* larvae are brooded and usually settle
23 within 4 hours of release; however, the larvae are initially photopositive and may swim up into

1 the water column, allowing for greater dispersal (Cancino et al., 1991). The hydroid *Clytia*
2 *hemisphaerica* is also a cosmopolitan species that grows quickly (Houliston et al., 2010) and
3 disperses via a medusa stage (Carré and Carré, 2000; Lucas et al., 1995). The anemone
4 *Metridium senile* has a planula larva (Bucklin, 1987a; Bucklin and Hedgecock, 1982) and is a
5 dense fouling organism on other hard substrata surrounded by soft-bottom habitats (Bucklin,
6 1987b; Meyer et al., 2017; Purcell, 1977).

7 Just adjacent to our study sites is a rocky reef inhabited by soft corals, sponges, ascidians,
8 and bryozoans. However, none of the common reef species recruited to our fouling panels. The
9 most common species on the reef have generally short pelagic larval duration and slow growth.
10 One of the most common reef species, *Balanophyllia elegans*, has a crawl-away larva that settles
11 just centimeters from the adult (Altieri, 2003). The octocoral *Swiftia spauldingi* has large eggs
12 and low fecundity, possibly indicating restricted dispersal (Feehan and Waller, 2015). The
13 ascidian *Metandrocarpa taylori* broods its larvae to the tadpole stage; tadpoles are demersal and
14 metamorphose within 1-10 hours of release (Abbott, 1955; Haven, 1971). For larvae, short-range
15 dispersal (< 1 km) may be an evolutionary stable strategy (Shanks et al., 2003). Dispersing only
16 a short distance away from the adult helps ensure that individuals will find a suitable substratum
17 on which to settle when competent, as hard substrata are widely spaced and there is no guarantee
18 of finding one when dispersing long distances (Grantham et al., 2003; Shanks et al., 2003).

19

20 4.4 Mobile fauna on the fouling panels

21 Similar to many of the sessile species, the mobile species that recruited to settlement
22 plates in this study all have long-duration planktotrophic larvae. All are also predators as adults.
23 The three nudibranchs, *Onchidoris bilamellata*, *Hermisenda crassicornis*, and *Pleurobranchaea*

1 *californica*, all have planktotrophic veliger larvae; *O. bilamellata* and *H. crassicornis* larvae
2 remain in the water column for 1 – 2 months (Arkett et al., 1989; Avila, 1998; Avila et al. 1996;
3 Barbeau et al., 2004; Chia and Koss, 1988; Gibson et al., 2003; Harrigan and Alkon, 1978).
4 Settlement of *O. bilamellata* and *H. crassicornis* is induced by the presence of their prey, which
5 includes barnacles (for *O. bilamellata*), hydroids, and the anemone *Metridium senile* (for *H.*
6 *crassicornis*), all of which were present on our panels (Avila, 1998; Avila et al., 1996, 1994).
7 *Pleurobranchaea californica* is also an opportunistic predator as an adult (Lee et al., 1974;
8 Yafremava et al., 2007). Given their small size, we speculate that the *O. bilamellata* and *H.*
9 *crassicornis* individuals observed on the fouling panels in this study are most likely new recruits.
10 *Onchidoris bilamellata* adults reach sexual maturity in as little as 2 months, and most survive
11 less than a year (Claverie and Kamenos, 2008; Todd, 1979). This species can also be
12 characterized as a fast-growing, short-lived pioneer species.

13 Turbellarians belonging to genus *Notocomplana* are predators (Koopowitz et al., 1976;
14 Phillips and Chiarappa, 1980) but have direct development (Rawlinson et al., 2008), making this
15 flatworm the only species observed on the settlement plates without a pelagic larval stage.
16 Gastropods in genus *Alia* are drill predators (Chattopadhyay and Baumiller, 2010), and *A.*
17 *gausapata* has planktotrophic larvae (Reitzel et al, 2004).

18

19 4.5 Community assembly on hard substrata

20 The hard substrata in this study were colonized by vastly different taxa than are present
21 on the adjacent rocky reef, but nevertheless featured a community with two trophic levels. Our
22 results suggest there may be a specialized assemblage of species that exploits isolated hard-
23 bottom habitats surrounded by sand; these habitats include crab and mollusk shells, the fouling

1 panels in this study, and likely any new anthropogenic installations. The species recruiting to
2 hard-bottom habitats surrounded by sand can be generally characterized as pioneer species with
3 long-duration planktotrophic larvae and fast growth, in contrast to the most abundant species on
4 the reef. Anthropogenic substrata are thus unlikely to function as “stepping-stones.”

5 The recruitment of *Hesperibalanus hesperius* was influenced by oceanographic
6 conditions leading to larval retention. For other species, it is difficult to say whether settlement
7 patterns were influenced by succession, phenology, or interannual variation, as these factors
8 were compounded. Species occurring in higher abundance on 79-day panels (*Metridium senile*,
9 *Alia gausapata*) may have just had higher overall recruitment in 2015 compared to 2014, and we
10 cannot definitively describe them as belonging in mid- or late-succession stages. Species
11 recruiting in higher abundance during deployments C and D in August – October 2014
12 (*Onchidoris bilamellata*, *Notocomplana* sp.) may have been influenced by their phenology.
13 Subtidal populations of *O. bilamellata* spawn in July (Claverie and Kamenos, 2008), so
14 competent larvae would recruit in September – October. To our knowledge, the timing of
15 recruitment for *Notocomplana* sp. in the eastern Pacific is undocumented, though juveniles have
16 been found on fouling substrata collected in September – October (Gartner, 2010).

17 Many of the mobile species in this study are known predators of sessile species that
18 recruited to the panels and settle in response to chemical cues from their prey. Our study may
19 thus provide an example of facilitation in succession, with prey species facilitating the
20 establishment of mobile species. The results of this study are preliminary, but our observations
21 raise many questions about the effect of distance from a source population on recruitment and
22 assembly of subtidal hard-bottom communities.

23

1 Acknowledgments

2 This material is based upon work supported by the National Science Foundation Graduate
3 Research Fellowship Program under Grant No. DGE-0829517. Numerous volunteers and OIMB
4 staff assisted with mooring construction, deployment, and recovery. Special thanks to L. Draper
5 for piloting R/V *Pluteus* and for relentless patience. YL is partially supported by the Dr. George
6 Grice Postdoctoral Scholarship from Woods Hole Oceanographic Institution, with support from
7 NSF grant #1634965.

8

9 References

- 10 Abbott, D.P., 1955. Larval structure and activity in the ascidian *Metandrocarpa taylori*. J.
11 Morphol. 97, 569–593.
- 12 Altieri, A.H., 2003. Settlement cues in the locally dispersing temperate cup coral *Balanophyllia*
13 *elegans*. Biol. Bull. 204, 241–245.
- 14 Arkett, S.A., Chia, F.-S., Goldberg, J.I., Koss, R., 1989. Identified settlement receptor cells in a
15 nudibranch veliger respond to specific cue. Biol. Bull. 176, 155–160.
- 16 Avila, C., 1998. Competence and metamorphosis in the long-term planktotrophic larvae of the
17 nudibranch mollusc *Hermisenda crassicornis* (Eschscholtz, 1831). J. Exp. Mar. Bio. Ecol.
18 231, 81–117.
- 19 Avila, C., Arigue, A., Tamse, C.T., Kuzirian, A.M., 1994. *Hermisenda crassicornis* larvae
20 metamorphose in laboratory in response to artificial and natural inducers. Biol. Bull. 187,
21 252–253.
- 22 Avila, C., Tamse, C.T., Kuzirian, A.M., 1996. Induction of metamorphosis in *Hermisenda*
23 *crassicornis* larvae (Mollusca: Nudibranchia) by GABA, choline, and serotonin. Invertebr.
24 Reprod. Dev. 29, 127–141.
- 25 Barbeau, M.A., Durelle, K., Aiken, R.B., 2004. A design for multifactorial choice experiments:
26 an example using microhabitat selection by sea slugs *Onchidoris bilamellata* (L.). J. Exp.
27 Mar. Bio. Ecol. 307, 1–16.
- 28 Barnes, H., Barnes, M., 1959. The naupliar stages of *Balanus hesperius* Pilsbry. Can. J. Zool. 37,
29 237–244.
- 30 Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral
31 reefs. Science 292, 1532–1535.
- 32 Bergmann, M., Gutow, L., Klages, M., 2015. Marine Anthropogenic Litter. Springer,
33 Heidelberg.
- 34 Berntsson, K., Jonsson, P., Lejhall, M., Gatenholm, P., 2000. Analysis of behavioural rejection
35 of micro-textured surfaces and implications for recruitment by the barnacle *Balanus*
36 *improvisus*. J. Exp. Mar. Bio. Ecol. 251, 59–83.

- 1 Berntsson, K.M., Jonsson, P.R., 2003. Temporal and spatial patterns in recruitment and
2 succession of a temperate marine fouling assemblage: a comparison of static panels and
3 boat hulls during the boating season. *Biofouling* 19, 187–195.
- 4 Boessenecker, R.W., 2013. Taphonomic implications of barnacle encrusted sea lion bones from
5 the Middle Pleistocene Port Orford Formation, coastal Oregon. *J. Paleontol.* 87, 657–663.
- 6 Bram, J.B., Page, H.M., Dugan, J.E., 2005. Spatial and temporal variability in early successional
7 patterns of an invertebrate assemblage at an offshore oil platform. *J. Exp. Mar. Bio. Ecol.*
8 317, 223–237.
- 9 Bucklin, A., 1987a. Growth and asexual reproduction of the sea anemone *Metridium*:
10 comparative laboratory studies of three species. *J. Exp. Mar. Bio. Ecol.* 110, 41–52.
- 11 Bucklin, A., 1987b. Adaptive advantages of patterns of growth and asexual reproduction of the
12 sea anemone *Metridium senile* (L.) in intertidal and submerged populations. *J. Exp. Mar.*
13 *Bio. Ecol.* 110, 225–243.
- 14 Bucklin, A., Hedgecock, D., 1982. Biochemical genetic evidence for a third species of
15 *Metridium* (Coelenterata: Actinaria). *Mar. Biol.* 66, 1–7.
- 16 Cancino, J.M., Hughes, R.N., 1987. The effect of water flow on growth and reproduction of
17 *Celleporella hyalina* (L.) (Bryozoa: Cheilostomata). *J. Exp. Mar. Bio. Ecol.* 112, 109–130.
- 18 Cancino, J.M., Hughes, R.N., Ramirez, C., 1991. Environmental cues and the phasing of larval
19 release in the bryozoan *Celleporella hyalina* (L.). *Proc. R. Soc. B* 246, 39–45.
- 20 Capet, X., Colas, F., Penven, P., Marchesiello, P., McWilliams, J.C., 2008. Eddies in eastern-
21 boundary subtropical upwelling systems. *Ocean Model. an Eddying Regime* 1567, 131–147.
- 22 Carlton, J.T., 2007. *The Light and Smith manual: intertidal invertebrates from central California*
23 *to Oregon*, Fourth ed. University of California Press.
- 24 Carré, D., Carré, C., 2000. Origin of germ cells, sex determination, and sex inversion in medusae
25 of the genus *Clytia* (Hydrozoa, leptomedusae): the influence of temperature. *J. Exp. Zool.*
26 287, 233–42.
- 27 Chalmer, P.N., 1982. Settlement patterns of species in a marine fouling community and some
28 mechanisms of succession. *J. Exp. Mar. Bio. Ecol.* 58, 73–85.
- 29 Chassignet, E.P., Hurlburt, H.E., Smedstad, O.M., Halliwell, G.R., Hogan, P.J., Wallcraft, A.J.,
30 Baraille, R., Bleck, R., 2007. The HYCOM (HYbrid Coordinate Ocean Model) data
31 assimilative system. *J. Mar. Syst.* 65, 60–83.
- 32 Chattopadhyay, D., Baumiller, T.K., 2010. Effect of durophagy on drilling predation: a case study
33 of Cenozoic molluscs from North America. *Hist. Biol.* 22, 367–379.
- 34 Chia, F.-S., Koss, R., 1988. Induction of settlement and metamorphosis of the veliger larvae of
35 the nudibranch, *Onchidoris bilamellata*. *Int. J. Invertebr. Reprod. Dev.* 14, 53–70.
- 36 Chiswell, S.M., Booth, J.D., 1999. Rock lobster *Jasus edwardsii* larval retention by the
37 Wairarapa Eddy off New Zealand. *Mar. Ecol. Prog. Ser.* 183, 227–240.
- 38 Chiswell, S.M., Roemmich, D., 1998. The East Cape Current and two eddies: A mechanism for
39 larval retention? *New Zeal. J. Mar. Freshw. Res.* 32, 385–397.
- 40 Claverie, T., Kamenos, N.A., 2008. Spawning aggregations and mass movements in subtidal
41 *Onchidoris bilamellata* (Mollusca: Opisthobranchia). *J. Mar. Biol. Assoc. UK* 88, 157–159.
- 42 Crimaldi, J.P., Thompson, J.K., Rosman, J.H., Lowe, R.J., Koseff, J.R., 2002. Hydrodynamics of
43 larval settlement: the influence of turbulent stress events at potential recruitment sites 47,
44 1137–1151.
- 45 De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal
46 dynamics of the epifauna community on offshore wind farm foundations and their role as

- 1 stepping stones for non-indigenous species. *Hydrobiologia* 756, 37–50.
- 2 Elwood, D., Yim, S.C., Prudell, J., Stillinger, C., von Jouanne, A., Brekken, T., Brown, A.,
3 Paasch, R., 2010. Design, construction, and ocean testing of a taut-moored dual-body wave
4 energy converter with a linear generator power take-off. *Renew. Energy* 35, 348–354.
- 5 Feehan, K. a., Waller, R.G., 2015. Notes on reproduction of eight species of Eastern Pacific cold-
6 water octocorals. *J. Mar. Biol. Assoc. UK* 95, 691–696.
- 7 García, C.B., Moreno, I., 1998. Recruitment, growth, mortality and orientation patterns of
8 *Balanus trigonus* (Crustacea: Cirripedia) during succession on fouling plates. *Sci. Mar.* 62,
9 59–64.
- 10 Gartner, H., 2010. Subtidal invertebrate fouling communities of the British Columbian coast.
11 M.S. thesis, University of Victoria.
- 12 Gibson, G.D., 2003. Larval development and metamorphosis in *Pleurobranchaea maculata*, with
13 a review of development in the Notaspidea (Opisthobranchia). *Biol. Bull.* 205, 121–132.
- 14 Grantham, B.A., Eckert, G.L., Shanks, A.L., 2003. Dispersal potential of marine invertebrates in
15 diverse habitats. *Ecol. Appl.* 13, 108–116.
- 16 Gunderson, D.R., Parma, A.M., Hilborn, R., Cope, J.M., Fluharty, D.L., Miller, M.L., Vetter,
17 R.D., Heppell, S.S., Greene, H.G., 2008. The challenge of managing nearshore rocky reef
18 resources. *Fisheries* 33, 172–179.
- 19 Hadfield, M.G., 1986. Settlement and recruitment of marine invertebrates: a perspective and
20 some proposals. *Bull Mar Sci* 39, 418–425.
- 21 Harrigan, J.F., Alkon, D.L., 1978. Larval rearing, metamorphosis, growth and reproduction of
22 the eolid nudibranch *Hermisenda crassicornis* (Eschscholtz, 1831) (Gastropoda:
23 Opisthobranchia). *Biol. Bull.* 154, 430–439.
- 24 Haven, N.D., 1971. Temporal patterns of sexual and asexual reproduction in the colonial
25 ascidian *Metandrocarpa taylori* Huntsman. *Biol. Bull.* 140, 400–415.
- 26 Herz, L.E., 1933. The morphology of the later stages of *Balanus crenatus* Bruguiere. *Biol. Bull.*
27 64, 432–442.
- 28 Hills, J.M., Thomason, J.C., 1998. The effect of scales of surface roughness on the settlement of
29 barnacle (*Semibalanus balanoides*) cyprids. *Biofouling* 12, 57–69.
- 30 Hoare, K., Goldson, A.J., Giannasi, N., Hughes, R.N., 2001. Molecular phylogeography of the
31 cosmopolitan bryozoan *Celleporella hyalina*: cryptic speciation? *Mol. Phylogenet. Evol.* 18,
32 488–492.
- 33 Houlston, E., Momose, T., Manuel, M., 2010. *Clytia hemisphaerica*: A jellyfish cousin joins the
34 laboratory. *Trends Genet.* 26, 159–167.
- 35 Hudon, C., Bourget, E., Legendre, P., 1983. An integrated study of the factors influencing the
36 choice of the settling site of *Balanus crenatus* cyprid larvae. *Can. J. Fish. Aquat. Sci.* 40,
37 1186–1194.
- 38 Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of
39 benthic marine invertebrates. *Mar Ecol Prog Ser* 155, 269–301.
- 40 Hutchings, J.B., Pearce, A.F., 1994. Influence of the Leeuwin Current on recruitment of tropical
41 reef fishes at Rottenest Island, western Australia. *Bull. Mar. Sci.* 54, 245–255.
- 42 Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S., van Oppen, M.J.H., Willis,
43 B.L., 2009. Larval retention and connectivity among populations of corals and reef fishes:
44 history, advances and challenges. *Coral Reefs* 28, 307–325.
- 45 Keough, M.J., Raimondi, P.T., 1996. Responses of settling invertebrate larvae to bioorganic
46 films: effects of large-scale variation in films. *J. Exp. Mar. Bio. Ecol.* 207, 59–78.

- 1 Koehl, M., 2007. Mini review: hydrodynamics of larval settlement into fouling communities.
2 Biofouling 23, 357–368.
- 3 Koehl, M.A.R., Crimaldi, J.P., Dombroski, D.E., 2013. Wind chop and ship wakes determine
4 hydrodynamic stresses on larvae settling on different microhabitats in fouling communities.
5 Mar. Ecol. Prog. Ser. 479, 47–62.
- 6 Koopowitz, H., Silver, D., Rose, G., 1976. Primitive nervous systems. Control and recovery of
7 feeding behavior in the polyclad flatworm, *Notoplana acticola*. Biol. Bull. 150, 411–425.
- 8 Krone, R., Gutow, L., Joschko, T.J., Schröder, A., 2013. Epifauna dynamics at an offshore
9 foundation - Implications of future wind power farming in the North Sea. Mar. Environ.
10 Res. 85, 1–12.
- 11 Kulikova, V.A., Omelyanenko, V.A., 2005. Summer meroplankton of the northern part of
12 Amursky Bay (Peter the Great Bay, Sea of Japan). Ecol. Stud. State Ecosyst. Amur. Bay
13 Estuar. Zo. Razdolnaya River (Sea Japan) 2, 205–228.
- 14 Lee, C., Kim, C.-H., 1990. Larval development of *Balanus trigonus* Darwin (Cirripedia:
15 Thoracica: Balanidae) reared in the laboratory. Bull. Korean Fish. Soc. 23, 457–467.
- 16 Lee, R.M., Robbins, M.R., Palovcik, R., 1974. *Pleurobranchaea* behavior: food finding and
17 other aspects of feeding. Behav. Biol. 12, 297–315.
- 18 Lemire, M., Bourget, E., 1996. Substratum heterogeneity and complexity influence micro-
19 habitat selection of *Balanus* sp. and *Tubularia crocea* larvae. Mar. Ecol. Prog. Ser. 135, 77–
20 87.
- 21 Limouzy-Paris, C.B., Graber, H.C., Jones, D.L., Röpke, A.W., Richards, W.J., 1997.
22 Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida
23 Current. Bull. Mar. Sci. 60, 966–983.
- 24 Lobel, P.S., Robinson, A.R., 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian
25 waters. J. Plankton Res. 10, 1209–1223.
- 26 Lucas, C.H., Williams, D.W., Shearer, M., 1995. Seasonal dynamics and production of the
27 hydromedusan *Clytia hemisphaerica* (Hydromedusa, Leptomedusa) in Southampton water.
28 Estuaries 18, 362–372.
- 29 Meyer, K.S., Brooke, S.D., Sweetman, A.K., Wolf, M., Young, C.M., 2017. Invertebrate
30 communities on historical shipwrecks in the western Atlantic: relation to islands. Mar. Ecol.
31 Prog. Ser. 566: 17–29.
- 32 Miller, R.G., Hutchison, Z.L., Macleod, A.K., Burrows, M.T., Cook, E.J., Last, K.S., Wilson, B.,
33 2013. Marine renewable energy development: assessing the benthic footprint at multiple
34 scales. Front. Ecol. Environ. 11, 433–440.
- 35 Osman, R.W., 1977. The establishment and development of a marine epifaunal community.
36 Ecol. Monogr. 47, 37–63.
- 37 Ovsyannikova, I.I., Levin, V.S., 1982. Growth dynamics of barnacle *Solidobalanus hesperius* on
38 valves of Yezo scallop in conditions of bottom cultivation. Biol. Morya 4, 44–51.
- 39 Page, H.M., Culver, C.S., Dugan, J.E., Mardian, B., 2008. Oceanographic gradients and patterns
40 in invertebrate assemblages on offshore oil platforms. ICES J. Mar. Sci. 65, 851–861.
- 41 Percy, W.G., Stein, D.L., Hixon, M. a., Pikitch, E.K., Barss, W.H., Starr, R.M., 1989.
42 Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull. 87, 955–
43 965.
- 44 Perkol-Finkel, S., Benayahu, Y., 2009. The role of differential survival patterns in shaping coral
45 communities on neighboring artificial and natural reefs. J. Exp. Mar. Bio. Ecol. 369, 1–7.
- 46 Perkol-Finkel, S., Benayahu, Y., 2007. Differential recruitment of benthic communities on

- 1 neighboring artificial and natural reefs. J. Exp. Mar. Bio. Ecol. 340, 25–39.
- 2 Perkol-Finkel, S., Benayahu, Y., 2005. Recruitment of benthic organisms onto a planned
3 artificial reef: Shifts in community structure one decade post-deployment. Mar. Environ.
4 Res. 59, 79–99.
- 5 Perkol-Finkel, S., Shashar, N., Barneah, O., Ben-David-Zaslow, R., Oren, U., Reichart, T.,
6 Yacobovich, T., Yahel, G., Yahel, R., Benayahu, Y., 2005. Fouling reefal communities on
7 artificial reefs: Does age matter? Biofouling 21, 127–140.
- 8 Perkol-Finkel, S., Shashar, N., Benayahu, Y., 2006. Can artificial reefs mimic natural reef
9 communities? The roles of structural features and age. Mar. Environ. Res. 61, 121–135.
- 10 Phillips, D.W., Chiarappa, M.L., 1980. Defensive responses of gastropods to the predatory
11 flatworms *Freemania litoricola* (Heath and McGregor) and *Notoplana acticola* (Boone). J.
12 Exp. Mar. Bio. Ecol. 47, 179–189.
- 13 Pineda, J., Reyns, N.B., Starczak, V.R., 2009. Complexity and simplification in understanding
14 recruitment in benthic populations. Pop Ecol 51, 17–32.
- 15 Posey, M.H., Pregnall, A.M., Graham, R.A., 1984. A brief description of a subtidal Sabellariid
16 (Polychaeta) reef on the southern Oregon coast. Pacific Sci. 38, 28–33.
- 17 Purcell, J.E., 1977. Aggressive function and induced development of catch tentacles in the sea
18 anemone *Metridium senile* (Coelenterata, Actiniaria). Biol. Bull. 153, 355–368.
- 19 Rawlinson, K.A., Marcela Bolaños, D., Liana, M.K., Litvaitis, M.K., 2008. Reproduction,
20 development and parental care in two direct-developing flatworms (Platyhelminthes:
21 Polycladida: Acotylea). J. Nat. Hist. 42, 2173–2192.
- 22 Reitzel, A.M., Miner, B.G., McEdward, L.R., 2004. Relationships between spawning date and
23 larval development time for benthic marine invertebrates: a modeling approach. Mar. Ecol.
24 Prog. Ser. 280, 13–23.
- 25 Scruggs, J., Jacob, P., 2009. Harvesting ocean wave energy. Science 323, 1176–1178.
- 26 Shanks, A.L., 2001. An identification guide to the larval marine invertebrates of the Pacific
27 Northwest. Oregon State University Press, Corvallis.
- 28 Shanks, A.L., Grantham, B.A., Carr, M.H., 2003. Propagule dispersal distance and the size and
29 spacing of marine reserves. Ecol. Appl. 13, 159–169.
- 30 Silina, A. V., 2002. The effect of muddy bottom sediment on the abundance and life span of the
31 barnacle, *Hesperibalanus hesperius*, epizoic on scallop shells. Biofouling 18, 263–268.
- 32 Steimle, F.W., Zetlin, C., 2000. Reef habitats in the Middle Atlantic Bight: abundance,
33 distribution, associated biological communities, and fishery resource use. Mar. Fish. Rev.
34 62, 24–42.
- 35 Strub, P.T., Kosro, P.M., Huyer, A., 1991. The nature of the cold filaments in the California
36 Current System. J. Geophys. Res. 96, 14743.
- 37 Todd, C.D., 1979. The population ecology of *Onchidoris bilamellata* (L.) (Gastropoda:
38 Nudibranchia). J. Exp. Mar. Bio. Ecol. 41, 213–255.
- 39 Tuya, F., Boyra, A., Sanchez-Jerez, P., Barbera, C., Haroun, R., 2004. Can one species determine
40 the structure of the benthic community on a temperate rocky reef? The case of the long-
41 spined sea-urchin *Diadema antillarum* (Echinodermata: Echinoidea) in the eastern Atlantic.
42 Hydrobiologia 519, 211–214.
- 43 Wahl, M., 2009. Marine Hard Bottom Communities, Ecological Studies. Springer, Heidelberg.
- 44 Yafremava, L.S., Anthony, C.W., Lane, L., Campbell, J.K., Gillette, R., 2007. Orienting and
45 avoidance turning are precisely computed by the predatory sea-slug *Pleurobranchaea*
46 *californica* McFarland. J. Exp. Biol. 210, 561–569.

- 1 Zhukova, N. V., 2000. Fatty acid components of two species of barnacles, *Hesperibalanus*
2 *hesperius* and *Balanus rostratus* (Cirripedia), as indicators of food sources. *Crustaceana* 73,
3 513–518.
- 4 Zullo, V.A., Marincovich, L.J., 1990. Balanoid barnacles from the Miocene of the Alaska
5 Peninsula, and their relevance to the extant boreal barnacle fauna. *J. Paleontol.* 64, 128–135.
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45

Deployment	Date deployed	Date recovered	Days on seafloor	Sites	Blocks (panels) recovered
A1	2 Jul 2014	22 Jul 2014	21	1-5	10 (40)
A2	2 Jul 2014	12 Aug 2014	42	1-3	6 (23)
A3	2 Jul 2014	21 Aug 2014	51	4-5	3 (10)
B1	22 Jul 2014	12 Aug 2014	22	1-3	6 (24)
B2	22 July 2014	21 Aug 2014	31	4-5	3 (12)
C	12 Aug 2014	22 Sep 2014	42	1-3	5 (40)
D	21 Aug 2014	8 Oct 2014	40	4-5	2 (15)
E	26 May 2015	12 Aug 2015	79	1-5	4 (27)

1 Table 1. Deployment times and locations of fouling panel blocks along the southern Oregon
2 coast.

3

4

5

Deployment	A1	A2	A3	B1	B2	C	D	E
Days on seafloor	21	42	51	22	31	42	40	79
<i>Clytia hemisphaerica</i>	217	252	1040	86	206	196	14	158
<i>Celleporella hyalina</i>		7			1			
<i>Metridium senile</i>		2				4		21
cf. <i>Mytilus californianus</i>								3
Spirorbid	5		18		18			3
Bivalve		2						
<i>Hermisenda crassicornis</i>	1	5	2	1	2	19		
<i>Onchidoris bilamellata</i>						26	61	21
<i>Pleurobranchia californica</i>								2
<i>Alia gausapata</i>	3	1		1				1520
<i>Notocomplana</i> sp.						128	16	

6 Table 2. Total abundances of non-dominant sessile and mobile species on all panels in each
7 deployment. *Hesperibalanus hesperius* recruitment results are presented in Fig. 3.

8

9

10

11

12

13

1 Fig. 1. Fouling panel and cement block design. Rope is attached to a surface float (outside
2 picture). Photo by J. Reynolds.

3 Fig. 2. Sites where cement blocks with settlement plates were deployed off the southern Oregon
4 coast (60 m depth). Stippled area indicates rocky reef.

5 Fig. 3. Average number of *C. hemisphaerica* on fouling panels at each site during each
6 deployment. Error bars show 95% confidence intervals.

7 Fig. 4. Average number of *H. hesperius* on fouling panels at each site during each deployment.
8 Error bars show 95% confidence intervals.

9 Fig. 5. A, Sea surface height (m) and surface current during July – October 2014 and May –
10 August 2015. Red stars indicate location of fouling panels. White area represents the Oregon
11 coast. A scale vector of 1m/s for current is also shown. B, Sea surface height and bottom current
12 during July – October, 2014 and May – August, 2015.

13 Fig. 6. Spearman correlations for barnacle recruitment (pooled for all sites) and A, the
14 convergence index in surface waters; B, surface current; C, the convergence index for near-
15 bottom waters; and D, near-bottom current speed. Error bars show 95% confidence intervals.

16

17

18

19

20

21

22

23

1 Fig. 1



2

3

4

5

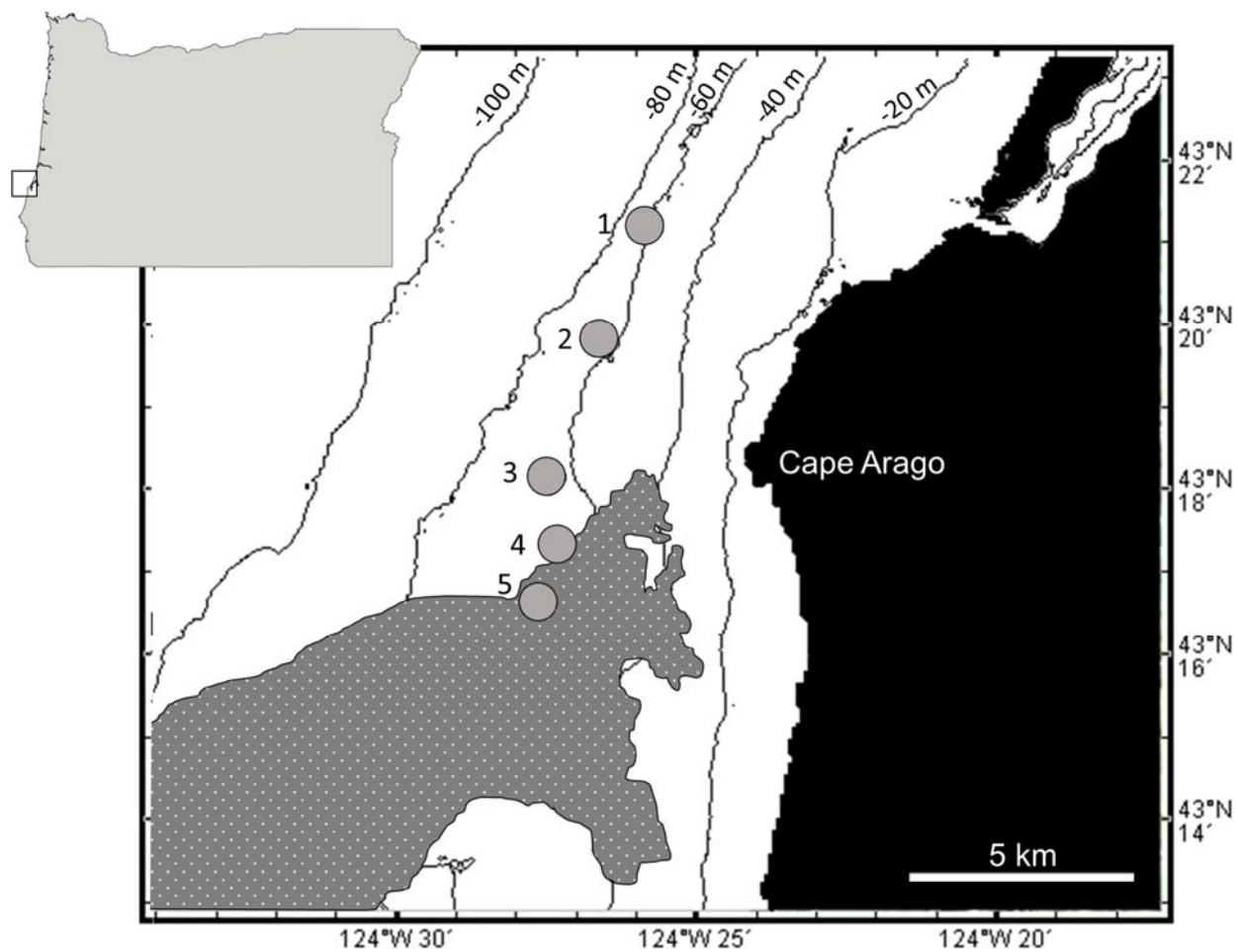
6

7

8

9

1 Fig. 2



2

3

4

5

6

7

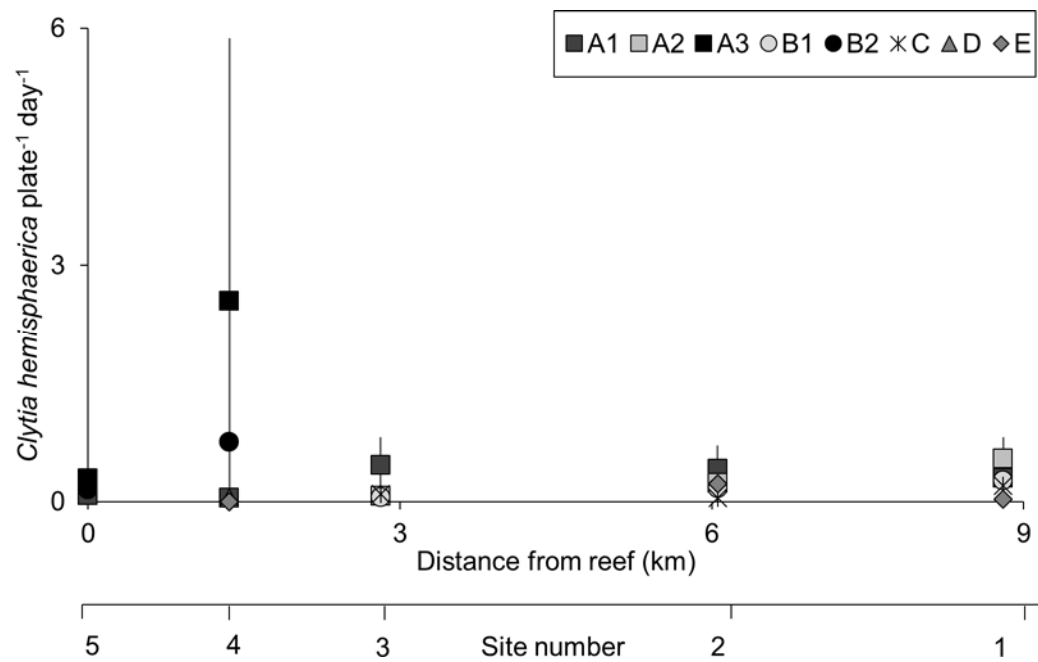
8

9

10

11

1 Fig. 3



2

3

4

5

6

7

8

9

10

11

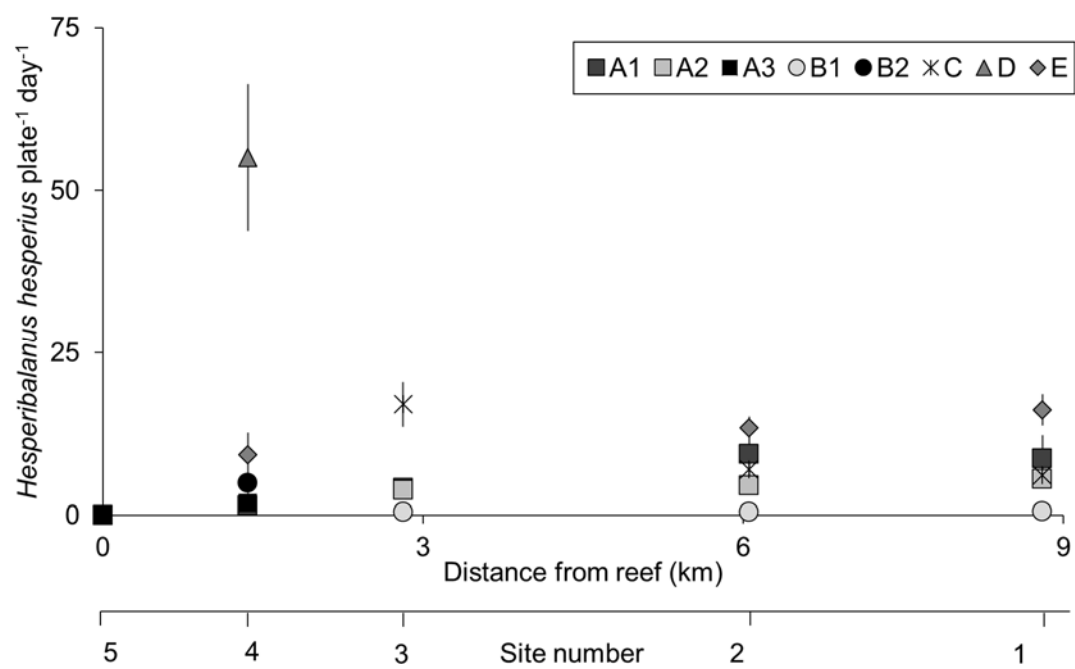
12

13

14

15

1 Fig. 4



2

3

4

5

6

7

8

9

10

11

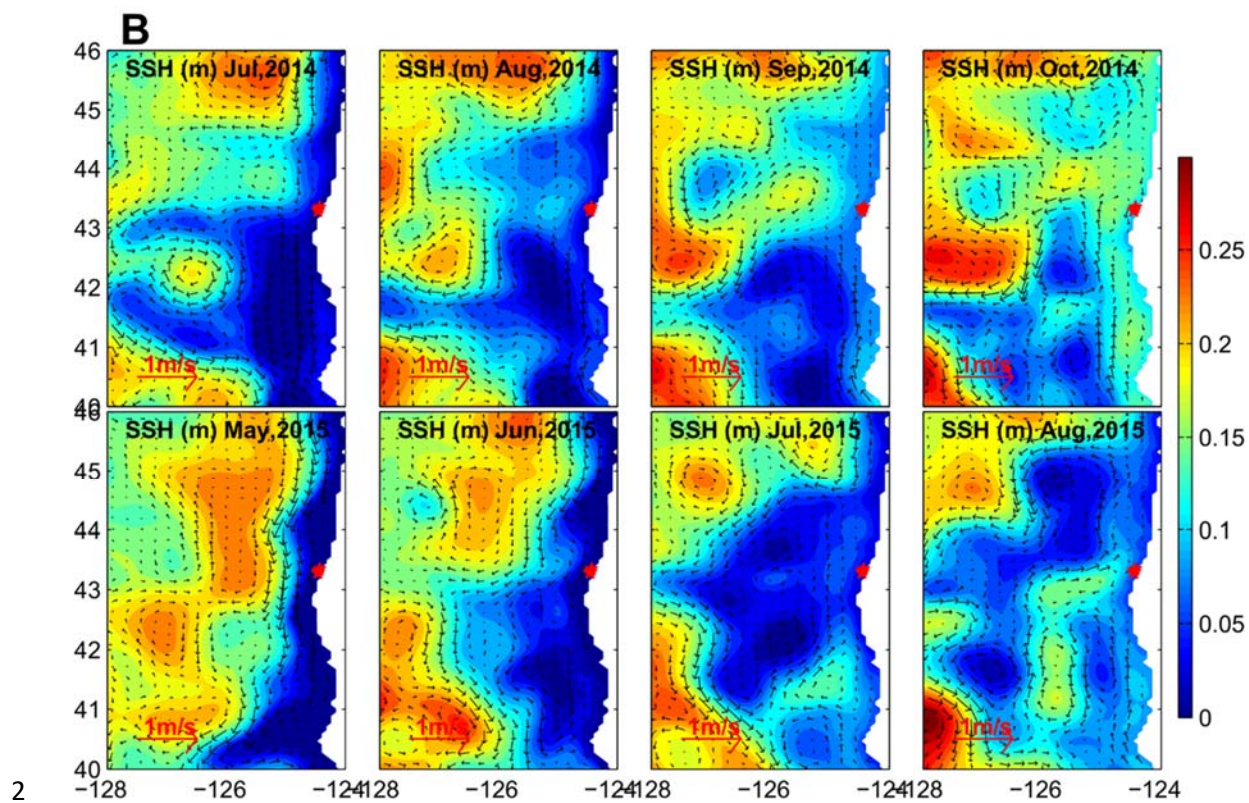
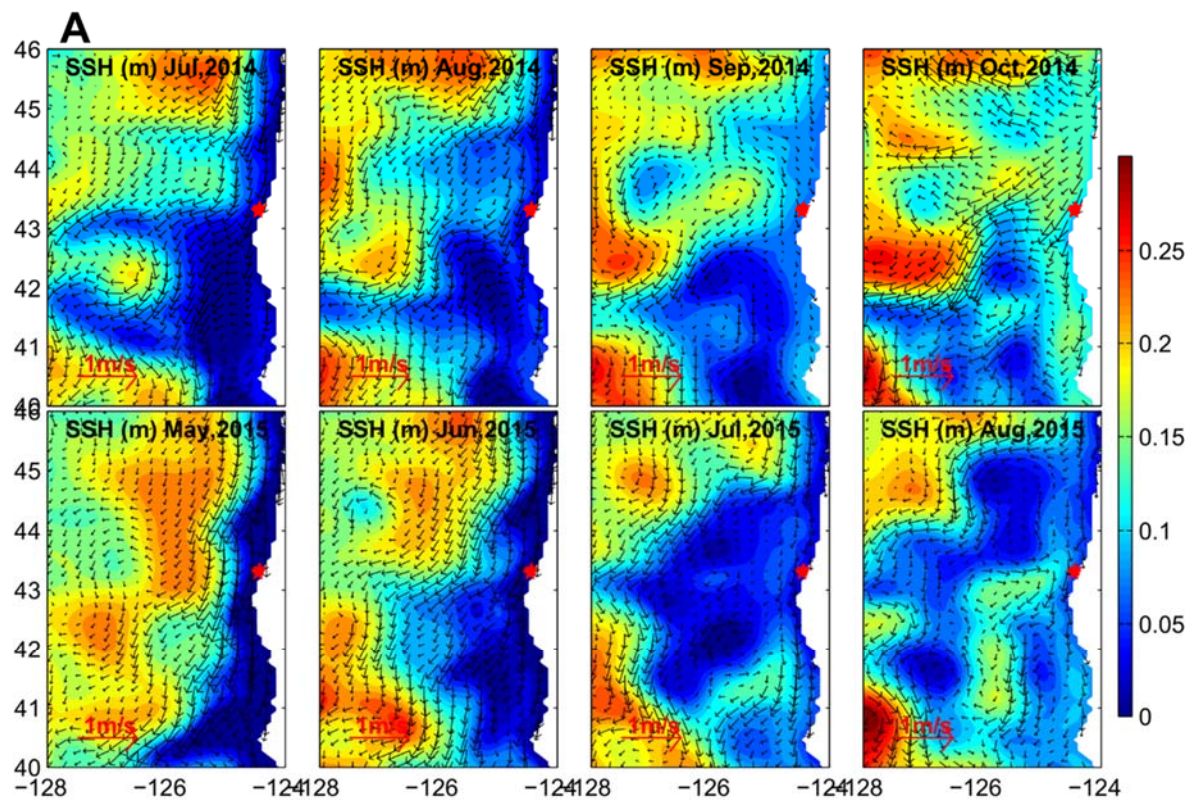
12

13

14

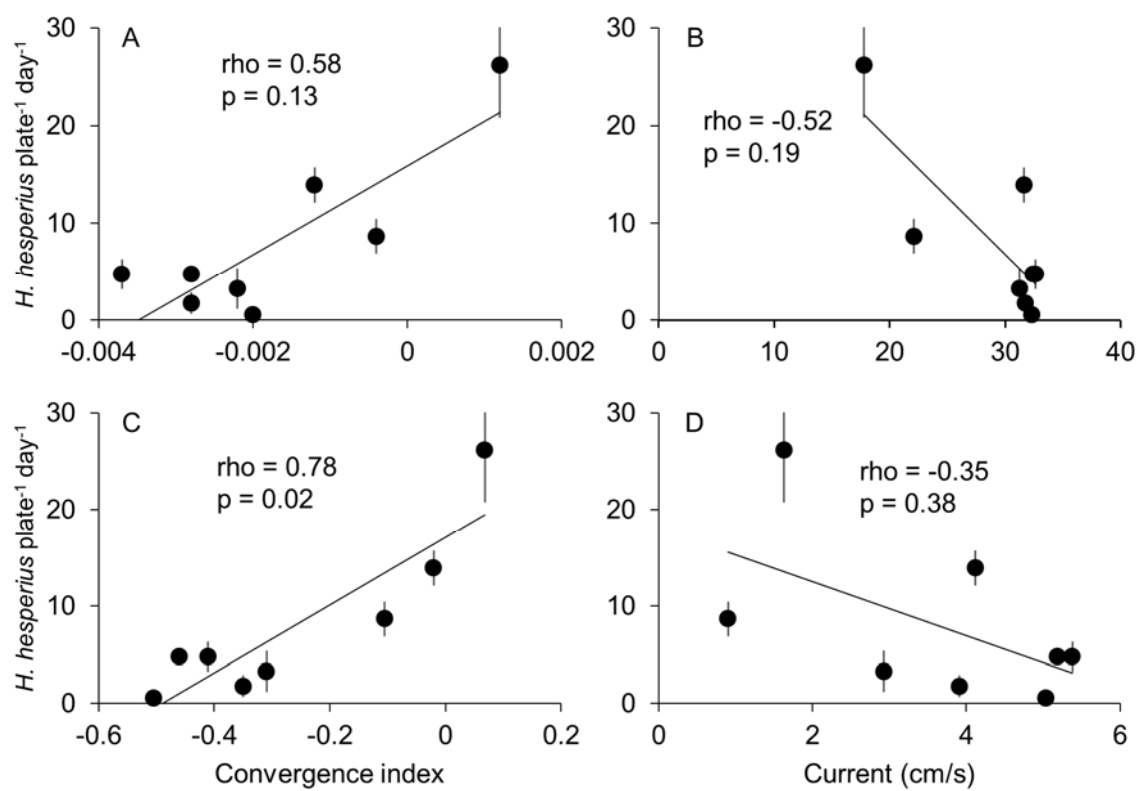
15

1 Fig. 5



2

1 Fig. 6



2