

## A COMPARISON OF DRAGON KELP, *EUALARIA FISTULOSA*, (PHAEOPHYCEAE) FECUNDITY IN URCHIN BARRENS AND NEARBY KELP BEDS THROUGHOUT THE ALEUTIAN ARCHIPELAGO<sup>1</sup>

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The Aleutian Archipelago coastal ecosystem has undergone a dramatic change in community composition during the past two decades. Following the removal of ~99% of the sea otters, *Enhydra lutris*, from the ecosystem, changes to the benthic communities resulted in widespread losses to most of the region's kelp beds and corresponding increases in the prevalence of urchin barrens. Within the urchin barrens, the few kelps that have remained are exposed to elevated light, nutrients and currents, all of which may enhance their physiological condition and thus result in greater fecundity. To explore this further, we examined patterns of sporophyte fecundity in the dominant canopy-forming kelp, *Eualaria fistulosa*, in both urchin barrens and in nearby kelp beds at seven Aleutian Islands spanning a range of 800 km. We found that the average weight of *E. fistulosa* sporophyll bundles was significantly greater on sporophytes occurring in the urchin barrens than in the nearby kelp beds. Furthermore, the average number of zoospores released per cm<sup>2</sup> of sporophyll area was also significantly greater in individuals from the urchin barrens than the nearby kelp beds. When these two metrics were combined, our results suggest that individual *E. fistulosa* sporophytes occurring in the urchin barrens may produce as many as three times more zoospores than individual *E. fistulosa* sporophytes occurring in the nearby kelp beds, and thus they may contribute disproportionately to the following year's sporophyte recruitment in both urchin barrens and the adjacent kelp beds.

**Key index words:** Aleutian Archipelago; *Eualaria fistulosa*; fecundity; kelp; urchin barren; zoospore

Patterns of zoospore release in kelps (Phaeophyceae, Laminariales) vary considerably with the physical and biological characteristics of their environment (Anderson and North 1967, Reed

1987, Reed et al. 1996, Graham 2003, Buschmann et al. 2004). For example, while some kelps synchronize zoospore release during periods of elevated hydrodynamic forces (e.g., Amsler and Neushul 1989, Reed et al. 1997), others release zoospores in response to seasonal changes in ocean nutrients, temperature and/or salinity (e.g., Reed et al. 1996, Buschmann et al. 2004). Still, zoospore release in other kelps can vary randomly at short (minutes to hours) time scales, but be tightly coupled with adult abundance at long (months to years) time scales (Graham 2003). Furthermore, this coupling between zoospore output and adult abundance can itself vary with kelp bed size and between the exterior and interior portions of the kelp bed due to differences in current flow and wave energy attenuation (Graham 2000, Reed et al. 2004). This combined with differences in kelp photosynthetic performance and nutrient uptake that can occur between the middle and outside the kelp beds (e.g., Gerard 1984) can impact overall zoospore production by individual kelp sporophytes. Given that zoospore production plays an integral role in the subsequent generation's sporophyte recruitment, identifying the processes that result in either increased local zoospore output and/or enhanced zoospore dispersal can be integral to understanding how kelp beds will recover following being lost or reduced by environmental perturbations.

Unlike many marine organisms, such as benthic invertebrates, that possess long distance dispersal stages that develop over time in the plankton (e.g., Scheltema 1971), kelp zoospores are typically viable immediately upon release and can settle on the seafloor within minutes, resulting in dispersal distances being limited to within a few meters of their parents (Reed et al. 1988, 1992, Santelices 1990, Gaylord et al. 2002). This can lead to deleterious problems associated with inbreeding among the resulting gametophytes and subsequent reduced fecundity in the following generation's sporophytes (Raimondi et al. 2004). However, while zoospore dispersal may be most limited near the center of the kelp beds, dispersal at the bed margins or from isolated individuals occurring outside the beds may be greater

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(e.g., Graham 2003) and thus play a larger role in the recovery of kelp populations that have been impacted by environmental perturbations and/or in the colonization of habitats where kelps have historically been absent (e.g., Reed et al. 2004). Nowhere may this be as important as in the Aleutian Archipelago where existing kelp beds have largely been lost or greatly reduced over a large geographic area due to overgrazing by sea urchins (Estes and Duggins 1995, Estes et al. 1998). In fact, the few kelp individuals that remain in areas where kelp beds have been lost may produce significantly more zoospores that exhibit greater dispersal distances than those individuals occurring in dense kelp beds, and thus they may play an important role in supporting the following year's recruitment both within the urchin barrens and nearby kelp beds.

The coastal ecosystems of the Aleutian Archipelago have historically been dominated by dense beds of the surface canopy kelp *Eualaria fistulosa* and several species of understory kelps in the genera *Saccharina*, *Laminaria*, and *Agarum*. Throughout the Archipelago, reduced predation on herbivores (i.e., sea otters feeding on sea urchins) initiated a shift in community composition from kelp beds to urchin-dominated barrens during the last two decades, with high herbivore pressure on the foliose macroalgae in the urchin barrens maintaining them (Estes et al. 1998). Although urchin barrens are currently far more abundant than kelp beds throughout the Aleutian Archipelago, some small isolated kelp beds exist adjacent to the urchin barrens, often with very distinct interfaces between them (Fig. 1; Konar 2000, Konar and Estes 2003, Konar et al. in review). In addition to these small beds, a few scattered *E. fistulosa* individual sporophytes exist within the urchin barrens where they are presumably exposed to reduced competition for light relative to individuals occurring within large kelp beds (e.g., Reed and Foster 1984, Edwards 1998, Clark et al. 2004). In

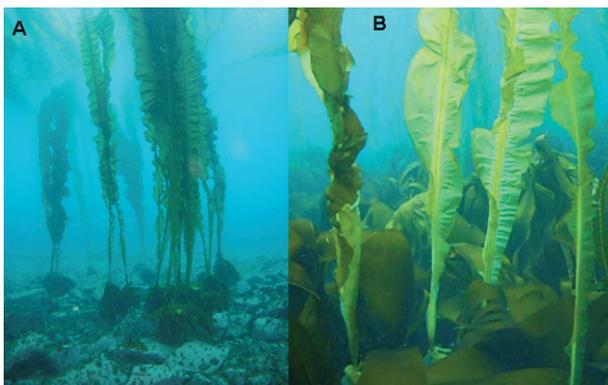


FIG. 1. Photographs of *Eualaria fistulosa* sporophytes and sub-surface kelps occurring in (A) urchin barrens and (B) dense kelp beds in the Aleutian Archipelago. Pictures highlight both the relative kelp density and show the sporophytes occurring in the barren grounds and on tops of boulders and/or pinnacles where urchins do not graze them.

addition, individuals occurring within the urchin barrens may also experience greater currents relative to individuals occurring within the dense kelp beds due to the attenuation of water flow by the kelps themselves (e.g., Jackson and Winant 1983, Jackson 1998, Hurd 2000, Hondolero 2011). Lastly, grazers that are far more abundant in the urchin barrens may themselves influence spore release by tearing the supporting tissues surrounding the sporangia as has been observed in amphipods feeding on red algae (e.g., Buschmann and Santelices 1987). These environmental and biological factors are known to impact kelp physiological condition (see reviews in North et al. 1986, Hurd 2000), and thus we hypothesize that *E. fistulosa* occurring within urchin barrens will exhibit greater photosynthetic rates and thus allocate greater energy toward zoospore production than *E. fistulosa* occurring within neighboring kelp beds (e.g., reviewed in Hurd 2000). While this remains untested in the field, if true, it could have important consequences to recruitment patterns within urchin barrens, especially when the nearest *E. fistulosa* kelp bed is tens to hundreds of meters away. Furthermore, if individuals occurring in urchin barrens produce more zoospores than their counterparts in neighboring kelp beds, they may contribute disproportionately to the following year's recruitment within the kelp beds as well, and thus ameliorate the effects of overall reduction in the species abundance throughout the Aleutian Archipelago.

#### METHODS

We examined differences in *Eualaria fistulosa* (Postels et Ruprecht) sporophyte fecundity between urchin barrens and adjacent kelp beds at seven islands in the Aleutian Archipelago (Fig. 2) during a cruise aboard the *RV Point Sur* in July 2010. At each island, the entire sporophyll bundles were collected from five haphazardly selected *E. fistulosa* sporophytes occurring within the urchin barrens (Fig. 1a) and five sporophytes occurring in the nearby kelp beds (Fig. 1b). The sporophyll

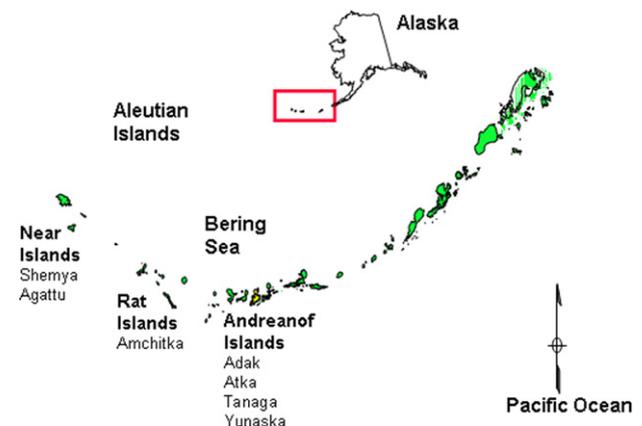


FIG. 2. Map of the Aleutian Archipelago showing the seven islands (sites) where urchin barrens and kelp beds were selected for this study.

bundles were placed in separate mesh bags and brought to the ship where they were weighed to estimate sporophyll mass per individual sporophyte within each habitat type. Following this, five haphazardly selected sporophylls from each bundle were removed and desiccated in the dark for 24h at 4°C. The following day, a single 3.5 cm<sup>2</sup> disk was cut from the middle of each sporophyll using a #12 stainless steel cork borer. The five disks from each sporophyll bundle (total sporophyll area = 17.5 cm<sup>2</sup>) were then placed together in 100 × 15 mm Fisherbrand Petri dishes (i.e., one dish per sporophyll bundle) filled with 30 mL of filtered seawater and allowed to release their zoospores in the dark for four hours. After four hours, the disks were removed and the zoospores mixed within each dish by repeatedly squeezing the bulb on the end of Pasteur pipette. Two drops of the zoospore solution were then placed on opposite sides of a Hausser Scientific Brightline hemacytometer. Zoospore density within the Petri dishes was then estimated by counting the number of zoospores in each of the 25–4 × 10<sup>-6</sup> mL squares per side on the hemacytometer (total sample volume = 2 × 10<sup>-4</sup> mL) using a compound microscope at 100×, and then extrapolating this to the entire 30 mL in the dishes. Following this, we estimated the relative potential number of zoospores that could be released by each sporophyll bundle (i.e., relative fecundity) by multiplying the average number of zoospores released per unit area of sporophyll by the total mass of each sporophyll bundle (Note: We were unable to precisely measure the weights of the five sporophyll disks per sporophyll bundle due to logistic constraints of working on a moving vessel at sea and consequently rely on total sporophyll bundle weight to assess differences in sporophyll mass). Thus, we were able to estimate (i) sporophyll mass per individual sporophyte, (ii) average #zoospores released per cm<sup>2</sup> sporophyll, and (iii) potential #zoospores per *E. fistulosa* sporophyte (i.e., relative fecundity) occurring within each habitat type.

## RESULTS

Sampling at seven sites (islands) spanning a 800-km range of the Aleutian Archipelago revealed that although *Eualaria fistulosa* sporophyte abundance was much greater within the kelp beds than in the urchin barrens (J. Estes, unpubl. data), the average sporophyll bundle weight was significantly greater on sporophytes in the urchin barrens than in the kelp beds (ANOVA:  $F_{1,6} = 5.214$ ,  $P = 0.062$ , Fig. 3a). Furthermore, although individual sporophyll bundle weights varied significantly among the study sites ( $F_{6,6} = 4.205$ ,  $P = 0.002$ ), the relative differences in sporophyll bundle weight between the habitat types themselves did not vary among the study sites (Habitat × Site interaction:  $F_{6,54} = 0.976$ ,  $P = 0.451$ , Table 1), suggesting that the sporophyll bundles were consistently larger on sporophytes within the urchin barrens than in the neighboring kelp beds. Specifically, the average weight of the sporophyll bundles in the urchin barrens was 608.39 g ± 84.51 (mean ± SE), while the average weight of the sporophyll bundles in the kelp beds was approximately one-half this value, or 380.14 g ± 90.18 (mean ± SE) (Fig. 3a). It is unclear whether this was due to the sporophytes simply being larger in the barren grounds or to the individual sporophytes exhibiting larger reproductive indices (i.e., sporophyll mass/

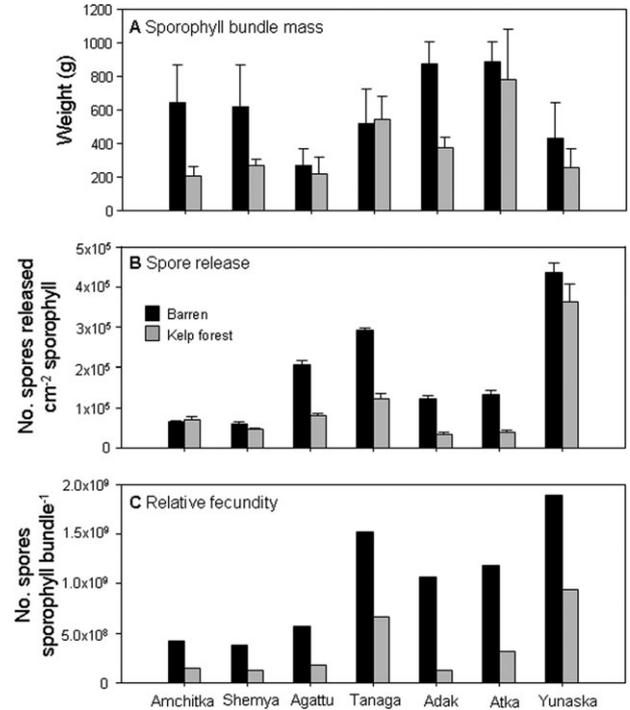


FIG. 3. Measures of *Eualaria fistulosa* sporophyte fecundity in the urchin barrens and adjacent kelp beds at all seven Aleutian Islands where this study was done. Data show differences in (A) average ( $\pm$  SE) weight of the sporophyll bundles on each sporophyte, (B) average ( $\pm$  SE) number of zoospores released per cm<sup>2</sup> sporophyll area, and (C) relative potential zoospore output (sporophyll weight × area-specific fertility) for *Eualaria fistulosa* sporophytes occurring in urchin barrens and adjacent kelp beds.

TABLE 1. Model III ANOVA (habitat = fixed, site = random) testing differences in sporophyll weight between the two habitats (urchin barrens and kelp beds) and seven islands in the Aleutian Archipelago.

Source	SOS	df	ms	F-ratio	P-value
Site	339,0000	6	5.65000	4.205	0.002
Habitat	684,000	1	684,000	5.214	0.062
Site × habitat	787,000	6	131,000	0.976	0.451
Error	7,260,000	56	134,000		

sporophyte mass) in the barren grounds. However, it is clear that the average number of zoospores released per cm<sup>2</sup> sporophyll as estimated in the hemacytometer was significantly greater for sporophylls collected from the urchin barren grounds than for sporophylls collected from the kelp beds (ANOVA:  $F_{1,6} = 61.01$ ,  $P < 0.001$ , Fig. 3b). As with sporophyll weight, this too varied significantly among study sites ( $F_{6,6} = 13.758$ ,  $P < 0.001$ ), but the relative differences in zoospore release between habitat types did not vary among study sites (Habitat × Site interaction:  $F_{6,54} = 0.822$ ,  $P = 0.557$ , Table 2). Finally, when the mass of the sporophyll bundles and the average zoospore output per cm<sup>2</sup> of sporophyll area were combined (i.e., #zoospores per unit area of sporophyll × sporophyll weight), the relative

TABLE 2 Model III ANOVA (habitat = fixed, site = random) testing differences in zoospore densities observed within the hemacytometer between the two habitat types (urchin barrens and kelp beds) and seven islands in the Aleutian Archipelago.

Source	SOS	df	ms	Fratio	Pvalue
Site	495.766	6	82.628	13.758	<0.001
Habitat	61.004	1	61.004	12.349	0.012
Site × habitat	29.646	6	4.941	0.823	0.557
Error	336.335	56	6.006		

potential zoospore output (relative fecundity) of *E. fistulosa* occurring in the urchin barrens was significantly greater than the relative potential zoospore output by *E. fistulosa* occurring in the kelp beds (paired *t*-test:  $t_6 = 5.29$ ,  $P = 0.018$ , Fig. 3c). Specifically, the relative potential zoospore output by *E. fistulosa* in the urchin barrens was approximately three times the relative potential zoospore output by *E. fistulosa* in the kelp beds. Altogether, while *E. fistulosa* is far more abundant within kelp beds, our data indicate that the individual sporophytes in the urchin barrens may contribute disproportionately to zoospore availability both within the urchin barrens and neighboring kelp beds.

#### DISCUSSION

The Aleutian Archipelago coastal ecosystem has undergone a dramatic change in community composition in the past two decades. Following the removal of ~99% of the sea otters, *Enhydra lutris*, from the ecosystem, changes to the benthic communities resulted in widespread losses of most kelp bed habitats and corresponding increases in the prevalence of urchin barrens (Estes and Duggins 1995, Estes et al. 1998). Consequently, the shallow coastal habitats of the Aleutian Archipelago are currently dominated by urchin barrens of the species *Strongylocentrotus polyacanthus*, with a few scattered *Eualaria fistulosa* kelp beds. Within the urchin barrens, however, a few isolated *E. fistulosa* individuals can occur on tops of rocks, small pinnacles, or other areas where they escape grazing (Konar 2000, Konar et al. in review). These often occur in the absence of other macroalgae and thus are generally exposed to increased irradiances and currents relative to those individuals occurring within nearby kelp beds. Consequently, this likely results in greater access to light and nutrients, which in turn may result in greater rates of photosynthesis (e.g., Gerard 1984, Edwards and Kim 2010) and nutrient uptake (e.g., Hurd et al. 1997), and thus promote greater energy allocation toward reproductive tissues (reviewed in Hurd 2000). While we did not measure irradiance or current flow in these two habitats, we rely on numerous investigations into the effects of kelp canopies on irradiance (e.g., Reed and Foster 1984, Kennelly 1989, Edwards 1998, Clark et al. 2004) and

current flow (e.g., Jackson and Winant 1983, Jackson 1998, Hondolero 2011) to assume that these were both greater in the urchin barrens than in the kelp beds, something that was supported by personal observations.

We found that two important fecundity metrics varied between the *Eualaria fistulosa* occurring in the urchin barrens versus the kelp beds. Specifically, sporophyll mass per individual *E. fistulosa* and average zoospore output per cm<sup>2</sup> of sporophyll were both greater in sporophytes occurring in the urchin barrens than those occurring in the adjacent kelp beds. Unfortunately, we did not measure individual sporophyte mass and thus cannot determine if these patterns were due to the sporophytes simply being larger in the barren grounds or if the reproductive indices (sporophyll mass/sporophyte mass) were greater in the barren grounds. Regardless, when these two metrics were combined (i.e., sporophyll mass per individual × zoospore output per unit area sporophyll), our results strongly indicate that relative potential *E. fistulosa* zoospore output per sporophyte was much greater, by a factor of three, in the urchin barrens than in the kelp beds. Interestingly, this pattern was observed at all seven sites spanning 800 km of the Aleutian Archipelago, suggesting that it is both widespread and general. While the reason for this is unclear, we believe that it may be due to elevated light and currents within the urchin barrens, as individuals do not compete as strongly for these resources as do individuals occurring in kelp beds (e.g., Gerard 1984). This may also result, at least in part, from increased grazing in the urchin barrens as has been observed in other macroalgae (e.g., Buschmann and Santelices 1987) although this remains untested.

Given the limited dispersal that many kelps exhibit (e.g., Reed et al. 1988, 1992, Raimondi et al. 2004), it is likely that the *Eualaria fistulosa* sporophytes occurring in the urchin barrens play an important role in any subsequent recruitment within that habitat as most macroalgal recruitment is supported by the recent settlement of zoospores (e.g., Hoffman 1987, Reed 1990, Santelices 1990, Norton 1992). However, recent studies have also shown that at least some kelps can rely on long-lived banks of dormant microscopic stages of mixed origins that accrue over time on the seafloor, ultimately reducing inbreeding and increasing their effective dispersal distances (Carney et al. in press). This, however, remains untested in this ecosystem. However, new sporophyte recruitment may not be as tightly coupled to local zoospore output within the urchin barrens due to increased currents relative to those within the kelp beds that likely result in enhanced dispersal distances (Jackson and Winant 1983, Reed et al. 2004). For example, Graham (2003) observed that while kelp zoospore output was tightly coupled to sporophyte abundance within the center of a large kelp bed when examined at seasonal to annual scales, it was decoupled with sporophyte abundance at the bed

margins due to greater current flow that disperse spores away from their place of release. This may be important in establishing kelp populations on newly exposed substrates or areas where kelps have been absent (Reed et al. 2004). However, the majority of kelps that recruit in the urchin barrens are presumably lost due to urchin grazing and thus the primary importance may be seen in recruitment within the existing kelp beds. If true, this may have significant consequences to the potential recovery of kelp beds in the Aleutian Archipelago following reductions in grazing, as was observed in the mid 20th century following the recovery of sea otter populations (Riedman and Estes 1990, Estes and Duggins 1995). While this may not be crucial to kelp recovery in the existing kelp beds because the total number of kelp individuals releasing zoospores is much greater than in the urchin barrens, it may be important in areas where extant kelp beds are largely absent or the kelps are in low abundance, which is the current state in the Aleutian Archipelago.

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- Amsler, C. D. & Neushul, M. 1989. Diel periodicity of spore release from the kelp *Nereocystis luetkeana* (Martens) Postels et Ruprecht. *J. Exp. Mar. Biol. Ecol.* 134:117–27.
- Anderson, E. K. & North, W. J. 1967. Zoospore release rates in giant kelp *Macrocystis*. *Bull. So. Cal. Acad. Sci.* 66:223–32.
- Buschmann, A. & Santelices, B. 1987. Micrograzers and spore release in *Iridaea laminarioides* Bory (Rhodophyta: Gigartinales). *J. Exp. Mar. Biol. Ecol.* 108:171–9.
- Buschmann, A. H., Vasquez, J. A., Osorio, P., Reyes, E., Filun, L., Hernandez-Gonzalez, M. C. & Vega, A. 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Mar. Biol.* 145:849–62.
- Carney, L. T., Bohonack, A. J., Edwards, M. S. & Alberto, F. in press. Genetic and experimental evidence for a mixed age, mixed origin bank of kelp microscopic stages in southern California. *Ecology*.
- Clark, R. P., Edwards, M. S. & Foster, M. S. 2004. Effects of shade from multiple kelp canopies on an understory algal assemblage. *Mar. Ecol. Prog. Ser.* 267:107–19.
- Edwards, M. S. 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). *J. Exp. Mar. Biol. Ecol.* 228:309–26.
- Edwards, M. S. & Kim, K. Y. 2010. Diel variation in photosynthetic performance in giant kelp *Macrocystis pyrifera* (Phaeophyceae, Laminariales) at different depths. *Aq. Bot.* 92:119–28.
- Estes, J. A. & Duggins, D. O. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.* 65:75–100.
- Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–86.
- Gaylord, B., Reed, D. C., Raimondi, P. T., Washburn, L. & McLean, S. R. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology* 83:1239–51.
- Gerard, V. A. 1984. The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. *Mar. Biol.* 84:189–95.
- Graham, M. H. 2000. Planktonic patterns and processes in the giant kelp *Macrocystis pyrifera*. PhD dissertation, UC San Diego, 160 pp.
- Graham, M. H. 2003. Coupling propagule output to supply at the edge and interior of a giant kelp forest. *Ecology* 84:1250–64.
- Hoffman, A. J. 1987. The arrival of seaweed propagules at the shore: a review. *Bot. Mar.* 30:151–65.
- Hondolero, D. E. 2011. Physical and biological characteristics of kelp forests in Kachemak Bay, Alaska. MS thesis, San Diego State University, 50 pp.
- Hurd, C. L. 2000. Water motion, marine macroalgal physiology, and production. *J. Phycol.* 36:453–72.
- Hurd, C. L., Stevens, C. L., Laval, B. E., Laval, G. A. & Harrison, P. J. 1997. Visualization of seawater flow around distinct forms of the giant kelp *Macrocystis integrifolia* from wave-sheltered and exposed sites. *Limnol. Oceanogr.* 42:156–63.
- Jackson, G. A. 1998. Currents in a high drag environment of a coastal kelp stand off California. *Cont. Shelf Res.* 17:1913–28.
- Jackson, G. A. & Winant, C. D. 1983. Effects of a kelp forest on coastal currents. *Cont. Shelf Res.* 2:75–80.
- Kennelly, S. J. 1989. Effects of kelp canopies on understory species due to shade and scour. *Mar. Ecol. Prog. Ser.* 50:215–24.
- Konar, B. 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia* 125:208–17.
- Konar, B. K., Edwards, M. S. & Estes, J. A. in review. Spatial and temporal persistence of alternate stable states in the coastal marine ecosystems of the Aleutian Archipelago. *Mar. Biol.*
- Konar, B. & Estes, J. A. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84:174–85.
- North, W. J., Jackson, G. A. & Manley, S. L. 1986. *Macrocystis* and its environment, knowns and unknowns. *Aq. Bot.* 26:9–26.
- Norton, T. A. 1992. Dispersal by macroalgae. *Br. Phycol. J.* 27:293–301.
- Raimondi, P. T., Reed, D. C., Gaylord, B. & Washburn, L. 2004. Effects of self-fertilization in the giant kelp, *Macrocystis pyrifera*. *Ecology* 85:3267–76.
- Reed, D. C. 1987. Factors affecting the production of sporophylls in the giant kelp *Macrocystis pyrifera* (L.) C.Ag. *J. Exp. Mar. Biol. Ecol.* 113:61–9.
- Reed, D. C. 1990. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* 71:776–87.
- Reed, D. C., Amsler, C. D. & Ebeling, A. W. 1992. Dispersal in kelps: factors affecting spore swimming and competency. *Ecology* 73:1577–85.
- Reed, D. C., Anderson, T. W., Ebeling, A. W. & Anghera, M. 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* 78:2443–57.
- Reed, D. C., Ebeling, A. W., Anderson, T. W. & Anghera, M. 1996. Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. *Ecology* 77:300–16.
- Reed, D. C. & Foster, M. S. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65:937–48.
- Reed, D. C., Laur, D. R. & Ebeling, A. W. 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58:321–35.
- Reed, D. C., Schroeter, S. C. & Raimondi, P. T. 2004. Spore supply and habitat variability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.* 40:275–84.
- Riedman, M. L. & Estes, J. A. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. *Biological Report 90(14)*, U.S. Fish and Wildlife Service. 126 pp.
- Santelices, B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Ann. Rev.* 28:177–276.
- Scheltema, R. S. 1971. The dispersal of the larvae of shallowwater benthic invertebrate species over long distances by ocean currents. In Crisp, D. J. [Ed.] *Fourth European Marine Biology Symposium*. Cambridge University Press, Cambridge, UK, pp. 7–28.