

## REVIEW

# Roles of transport and mixing processes in kelp forest ecology

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### Summary

**Fluid-dynamic transport and mixing processes affect birth, death, immigration and emigration rates in kelp forests, and can modulate broader community interactions. In the most highly studied canopy-forming kelp, *Macrocystis pyrifera* (the giant kelp), models of hydrodynamic and oceanographic phenomena influencing spore movement provide bounds on reproduction, quantify patterns of local and regional propagule supply, identify scales of population connectivity, and establish context for agents of early life mortality. Other analyses yield insight into flow-mediated species interactions within kelp forests. In each case, advances emerge from the use of ecomechanical approaches that propagate physical–biological connections at the scale of the individual to higher levels of ecological organization. In systems where physical factors strongly influence population, community or ecosystem properties, such mechanics-based methods promote crucial progress but are just beginning to realize their full potential.**

Key words: algal demographics, ecological biomechanics, giant kelp, kelp populations.

### Introduction

Mechanistic, physics-based approaches have a rich history of identifying themes in form and function (e.g. Wainwright et al., 1976; Vogel, 1994; Alexander, 2003), and defining relationships between organisms and their environments (e.g. Denny, 1988; Nicklas, 1992). Such approaches – often applied within a biomechanical or biophysical framework – have therefore advanced considerably our understanding of the ecology of individuals. Mechanics-based methods are less easily scaled up to address questions tied to populations, communities and ecosystems; nevertheless, they retain substantial utility in this regard when physical processes strongly influence demographic parameters, species interactions or aspects of nutrient cycling.

Some systems are especially amenable to connecting physical processes active at the scale of individuals to emergent properties of organism assemblages. Here, we focus on kelp forests and their relationship to coastal hydrodynamics. *Macrocystis pyrifera* (the giant kelp) (North, 1971) is a key habitat-forming macroalga distributed along the west coast of the Americas and Australasia that has been the subject of considerable scientific inquiry, and thus serves as a classic focal taxon. Early research on this species and others revealed the importance of water motion for algal growth (e.g. Neushul, 1972; Wheeler, 1980; Gerard, 1982) and the role of hydrodynamic forces in dictating seaweed mortality (e.g. Charters et al., 1969; Neushul, 1972; Norton et al., 1981). More recent work has further improved understanding of nutrient uptake at blade surfaces (Stevens and Hurd, 1997; Hurd, 2000), and has revealed nuances of the flow forces that act on macrophytes (Koehl, 1986; Carrington, 1990; Gaylord et al., 1994; Gaylord et al., 2003; Gaylord et al., 2008; Denny et al., 1998; Boller and Carrington, 2006). Many of these studies, however, have addressed algal–flow interactions largely at the level of a single organism. Far fewer studies have taken an ‘ecomechanics’ perspective (Wainwright et

al., 1976; Denny and Gaylord, 2010) (see also Denny, 2012) to explore how physical principles affecting individuals might drive trends at population, community or ecosystem scales. Analogous methods originating in physiological fields, such as environmental tolerance constructs (Kearney et al., 2012) and dynamic energy budget models (Nisbet et al., 2012), have received somewhat more use, albeit not yet in kelp systems.

In spite of the trend for mechanics-based kelp studies to focus on individual-level issues, there is clear potential for broader applicability. In any elementary demographic analysis, the change in number of individuals ( $N$ ) in a population between time  $t$  and  $t+1$  is given by:

$$N_{t+1} = N_t + B - D + I - E, \quad (1)$$

where  $B$ ,  $D$ ,  $I$  and  $E$  are the number of births, deaths, immigrants and emigrants, respectively. The biology of canopy-forming kelps like *Macrocystis* is such that there are multiple avenues by which physical processes influence terms on the right-hand side of Eqn 1. Among the most obvious are those affecting immigration and emigration rates, although all four parameters may be impacted. Kelps [i.e. brown algae of the order Laminariales (Abbott and Hollenberg, 1976)] produce reproductive propagules (microscopic spores) that serve as the primary agent of dispersal and have little capacity for swimming. Therefore, hydrodynamics dictate how far spores are carried, whether they exit their population of origin, and rates at which they enter adjacent populations. Properties of spore transport interact with other life history features as well. Most canopy-forming kelps have specific depth and substrate requirements, which confine them to locations where there is adequate light for growth and rocky seafloor for attachment. Especially for taxa that inhabit deeper, subtidal waters (5–30 m depth), these constraints encourage discontinuities in distribution, with populations growing as disjunct forests separated by expanses

of inhospitable sand. Kelp forests are also susceptible to hydrodynamic disturbance and poor growing conditions associated with low nutrients (Dayton and Tegner, 1984; Tegner and Dayton, 1987). This vulnerability causes individual forests to change dramatically in size through time, occasionally even blinking in and out of existence (Dayton et al., 1984). The overall network of forests is then sustained by the recovery of local populations by means of spore delivery from other beds. Canopy-forming species therefore operate in many ways like metapopulations [i.e. populations of populations (Levins, 1969; Reed et al., 2006)], where dispersal and connectedness are essential components of regional dynamics and long-term persistence. The importance of dispersal is further amplified by details of the kelp life cycle, where successful recruitment requires not simply delivery of spores to a destination site, but delivery of enough spores to exceed a minimum density. This point follows from how reproduction proceeds in kelps, with fusion of sperm and egg occurring through an elaborated process involving a second life stage. After the male or female spores disperse and settle, they develop into microscopic male or female gametophytes. The gametophytes in turn produce gametes that fertilize one another to yield the next generation of macroscopic adults. The fertilization step requires that gametophytes are located close enough to one another to enable the sperm to find the egg [i.e. within ~1 mm (Reed, 1990)].

The influence of physical factors on the movement and fate of kelp spores has direct bearing on the demographic rate parameters of Eqn 1. Below, we discuss how transport and mixing processes connect to each of them, as well as to other aspects of kelp ecology. We limit our attention to topics where physical drivers at the individual level scale up to inform higher-order ecological issues. Our discussion intentionally omits work on hydrodynamic implications for nutrient uptake and carbon fixation (which is focused mostly on physiological concerns), and long-term studies of oceanographic influences on kelp survivorship (which have not been merged with individual-level mechanics). We provide a brief sketch of physical factors whose roles ecomechanics helps quantify, identify sectors where physically based approaches have yielded fruit, and outline opportunities for future research.

### Transport and mixing processes influencing kelp population ecology

Canopy-forming kelps experience hydrodynamic and oceanographic processes that span a range of scales (Fig. 1). As sketched above, many of these processes influence movement of kelp spores in the water column. Others modulate delivery or export of waterborne commodities such as nutrients into or away from a forest, or affect interactions among organisms that inhabit kelp forests. Below we describe several relevant elements of kelp forest fluid dynamics.

#### Physical processes underlying dispersal

At microscopic levels, a key consideration for transport of kelp spores is the balance of forces that dictate how fast spores sink through still water. Kelp spores are tiny (5–7  $\mu\text{m}$  in diameter for *Macrocystis*), and from first principles, including application of Stokes' Law and knowledge of the high drag coefficients of small spheres (Vogel, 1994), it is clear that they will fall exceptionally slowly. Experiments indeed verify that *Macrocystis* spores sink at approximately  $1 \times 10^{-3} \text{ mm s}^{-1}$  in immobile seawater (Gaylord et al., 2002). This observation in turn has important consequences for how kelp spores interact with turbulent fluid motions, a primary agent of vertical mixing. If spores sink at negligible rates, then their

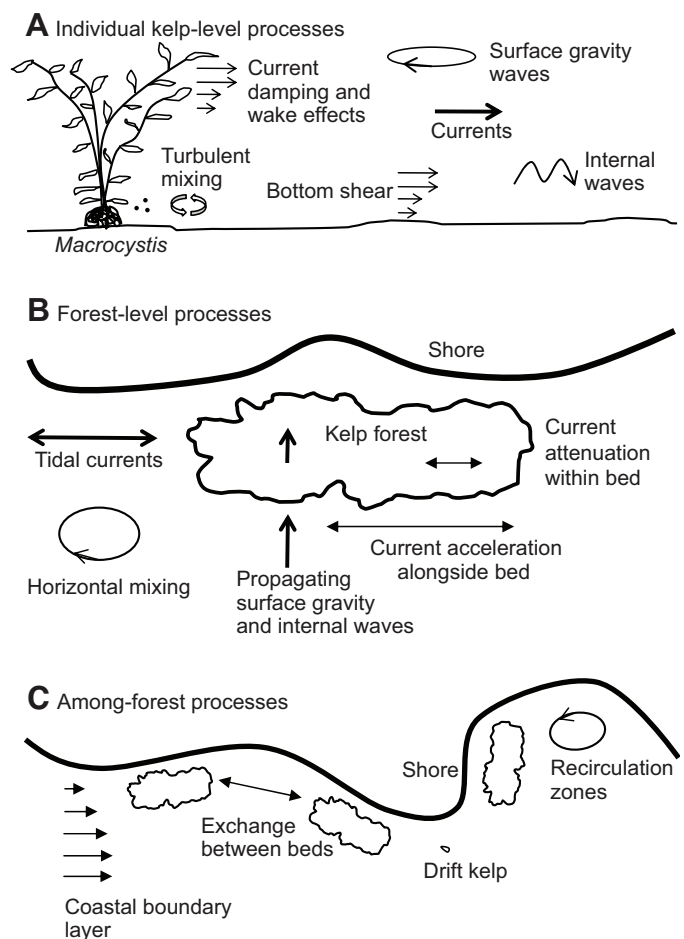


Fig. 1. Transport and mixing processes influencing kelp forests at various scales. (A) Fluid-dynamic processes operating at the level of, or in the vicinity of, individual kelps. (B) Larger-scale phenomenon that influence entire forests. (C) Oceanographic factors that drive exchange of propagules and materials among kelp forests.

transport to the seafloor is governed by mixing, and in fact speeded by this process (Denny and Shibata, 1989; McNair et al., 1997).

The efficiency of vertical mixing depends on the velocity and spatial scales of the turbulent fluid structures (eddies) that underlie it. From the perspective of predicting average patterns of spore movement, simple representations of mixing have utility. Spatial scales of mixing are constrained near the seafloor where the presence of a boundary limits eddy size, and this feature retards rapid mixing of spores (released in *M. pyrifera* from approximately 0.5 m above the bottom) into the overlying water column. At greater distances from the seafloor, spatial dimensions of fluid motion are bigger, and mixing across larger scales becomes easier. These physical issues are often encapsulated in eddy viscosity parameterizations that can be used to estimate the rate of spread of groups of spores vertically.

Quite simple representations of eddy viscosity ( $K$ ) are appropriate in some circumstances; for example, when only a steady current exists (Middleton and Southard, 1984). However, kelps grow at depths where wave-generated flows are also present. Waves create additional scales of motion that influence vertical mixing, particularly near the seafloor (Grant and Madsen, 1986). One eddy viscosity model that has shown utility in studies of spore

dispersal is (Gaylord et al., 2002; Gaylord et al., 2004; Gaylord et al., 2006):

$$K = \kappa z \left[ u_{*c}^2 \exp\left(-\frac{2z}{l_c}\right) + u_{*w}^2 \left(\frac{2z}{l_w}\right) \right]^{1/2}. \quad (2)$$

Here, the intensity of vertical mixing, as represented by  $K$ , varies strongly with distance above the seafloor,  $z$ . Velocity and length scales associated with both waves and an overarching current are included. Velocity scales are indexed by a wave friction velocity ( $u_{*w}$ ) and a current friction velocity ( $u_{*c}$ ), and length scales include one tied to waves ( $l_w$ ) and one tied to the current ( $l_c$ ). Table 1 indicates typical parameter values for nearshore regions. The coefficient  $\kappa$  is a constant, traditionally set to 0.4. Note that the above formulation does not capture the effects of kelps themselves on flow, and so applies best to conditions over the sand flats separating kelp forests. Its utility is greatest, therefore, for examining longer-distance components of spore dispersal.

The interaction of currents and waves with kelp also affects mixing. Turbulence is generated as flows pass obstructions, including elements of bottom topography and/or organisms themselves (e.g. bundles of kelp fronds). Dynamically scaled laboratory experiments suggest that within forests, mixing may be driven largely by wake turbulence, leading to eddy viscosities that vary little with height above the bottom and can be approximated as:

$$K = 0.1Ud, \quad (3)$$

as long as the magnitudes of wave-driven flow are not too large. Here,  $U$  is the velocity of the mean current inside the forest and  $d$  is the diameter of an average kelp frond bundle (Rosman et al., 2010). It is also possible for more organized fluid structures to arise in wakes, generating secondary flows that cause net transport in certain directions (Gaylord et al., 2004). An auxiliary issue is that turbulence interacts with vertical gradients in horizontal currents (in particular the tendency for current speeds to be slowed in the vicinity of the seafloor) to stretch and smear spore clouds horizontally through the phenomenon of shear dispersion (Denny, 1988).

Ultimately, processes controlling vertical mixing affect dispersal by influencing how long spores remain in the water column, and thereby the distances over which they are transported horizontally. Because spores that reach higher elevations above the seafloor often remain suspended in the water column for some time, they can be carried substantial distances before they eventually contact the seafloor. By contrast, spores that are swept immediately to the bottom by turbulence have the potential to settle very close to the adult that released them. It is worth noting that impacts of turbulent

mixing on spore dispersal are tied primarily to dilution and spreading of spore clouds. Such effects are conceptually distinct from the coalescence phenomenon that affects external fertilization immediately following gamete release (Crimaldi, 2012).

#### Forest-wide delivery and exchange processes

At the scale of a whole kelp forest, there are additional factors that influence the movement of spores and other waterborne commodities. Coastal currents are slowed by the presence of the forest, such that horizontal flows inside may be attenuated by an order of magnitude or more (Fig. 2) (see also Jackson and Winant, 1983). This attenuation is dependent on the size of the forest and the density of plants. The hydrodynamic resistance of the forest also encourages arriving water masses to diverge and move around the sides of the forest. Such redirections can create regions of locally faster flow along a forest's offshore edge (Gaylord et al., 2007). Larger-scale pressure gradients associated with changes in speed and direction can additionally establish second-order, offshore flows within the forest. Internal waves and bores that propagate on density discontinuities in the water column may drive cross-shore currents that move in opposite directions in different depth strata (Jackson, 1984; Leichter et al., 1998; Rosman et al., 2007). Importantly, a number of the above transport and mixing processes are interconnected. For instance, current attenuation arising in a forest decreases mixing intensities (Eqn 3), which in turn reduces the ability of turbulence to overcome stratification. The latter feature facilitates propagation of internal waves. At larger geographic distances appropriate for assessing connectivity among populations, mesoscale oceanographic structures become relevant agents of transport and mixing (e.g. Bassin et al., 2005).

Although an aside, it is worth noting that a number of issues analogous to those governing kelp spore movement influence dispersal of terrestrial seeds. Wind-driven vertical mixing that drives seed uplift mimics similar phenomena in the marine environment (Nathan et al., 2002; Katul et al., 2005). Canopy drag in terrestrial forests causes flow attenuation and modifies mixing profiles much as in kelp systems, altering distances to which seeds are carried (Nathan and Katul, 2005). Seeds are preferentially released from trees in faster winds, just as initial phases of kelp spore transport depend on velocities local to a parent plant (Soons and Bullock, 2008). Although our discussion does not elaborate on such parallels, they are extensive, and hint at the potential for cross-fertilization of ideas.

#### Insights from the mechanistic approach

All of the above fluid-dynamic processes have implications for the population ecology of kelp forests. Hydrodynamic factors that bear

Table 1. Typical hydrodynamic parameter values used in Eqns 2 and 4, based on physical conditions commonly observed off the coast of southern California (after Gaylord et al., 2002; Gaylord et al., 2006)

Mathematical expression	Parameter	Units	Value
Coupled wave–current vertical eddy viscosity profile (Eqn 2) <sup>a</sup>	$u_{*c}$	$\text{m s}^{-1}$	0.002–0.10
	$u_{*w}$	$\text{m s}^{-1}$	0.02–0.25
	$l_c$	m	2.5–15
	$l_w$	m	0.02–0.70
Lognormal-Gaussian dispersal distribution (Eqn 4)	$a$	n/a	1.7–1.8
	$b$	n/a	15–30
	$c$	n/a	$22173U+676^b$

<sup>a</sup>Note that the four parameters associated with this expression are linked to at least some degree. Thus certain ranges of one parameter may be tied to certain ranges of another.

<sup>b</sup> $U$  is the mean depth-averaged current ( $\text{m s}^{-1}$ ) over the dispersal period.

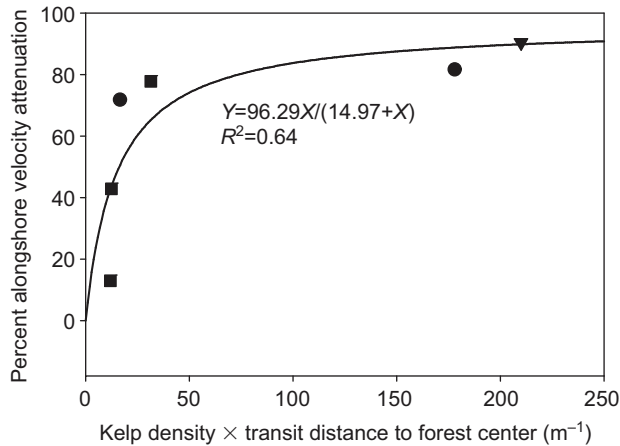


Fig. 2. Percent alongshore velocity attenuation in kelp forests, as a function of the product of kelp density (individuals  $m^{-2}$ ) and alongshore distance to the center of a forest (m). Data points were recalculated from measurements made in previous studies: triangle (Jackson, 1998); squares (Rosman et al., 2007); circles (Gaylord et al., 2007).

directly on spore dispersal dictate the fractions of spores that settle within a source forest (a measure of retained local births), the fractions that are transported away (emigrants), and the associated probability that spores will alight at a given density in a nearby forest (becoming immigrants there). Associated processes tied to self-fertility in kelps may affect patterns of density-dependent, early-life mortality (driving local deaths). Below, we highlight recent work addressing these issues. The vignettes that follow do not represent general coverage of the literature on kelp forests [for broad reviews of this nature, see Schiel and Foster (Schiel and Foster, 2006) and Graham et al. (Graham et al., 2007)]. Instead, we focus on studies that have advanced understanding of kelp forest systems by integrating physics and ecology. Findings group into several categories.

#### Dispersal and connectivity

Physical processes driving spore transport have clear implications for determining immigration and emigration rates to and from kelp forests ( $I$  and  $E$  in Eqn 1). It is now recognized that although many kelp spores disperse only a few meters (the traditional perspective for many years) (reviewed in Dayton, 1985), a substantial subset are also carried to far greater distances (Reed et al., 1988; Gaylord et al., 2002; Gaylord et al., 2006). This latter feature emerges from the fact that spore dispersal distributions are ‘fat-tailed’, much as has been recognized for seed dispersal in terrestrial systems (Levin et al., 2003; Gaylord et al., 2006; Nathan et al., 2011). It is possible that this characteristic is a general consequence of randomized transport motions operating at different scales along different directional axes. Modest rates of vertical turbulent mixing ensure that it can take a long time for spores that become suspended high in the water column to again be mixed down the several meters it would take to reach the seafloor. The substantially longer times to settle from such heights foster greater exposure to horizontal motions – themselves operating at scales of 10s to 1000s of meters – that disperse spores laterally. The combined effects of both processes generate a much broader tail in the distribution than would otherwise arise.

Because of the fat-tailed nature of the dispersal distribution, mean transport distances can be insufficient metrics of how far spores are commonly carried. Appreciable fractions of spores may

be swept to distances that are orders of magnitude beyond the mean, extending out to multiple kilometers (Gaylord et al., 2002; Gaylord et al., 2006). This point also means, again in the context of kelp population connectivity, that reproductively viable, dislodged adult plants (i.e. drifters that can release spores as they translate alongshore) (Dayton, 1985; Macaya et al., 2005; Hernández-Carmona et al., 2006) may not be required to explain regional population exchange (see also Reed et al., 2004). Such drifters must continue to be considered, of course, in cases of very long distance connectivity, especially over continental or hemispheric scales relevant for understanding biogeographic and evolutionary patterns (Dayton, 1985; Graham et al., 2007).

In *Macrocystis*, it has proven possible to develop quantitative expressions for dispersal distributions using ecomechanical methods (Gaylord et al., 2006). These methods combine fieldwork with physically based analyses to provide simplified expressions for patterns of dispersal. For example, approximating dispersal as a radial-symmetric process, the probability that a spore settles within an infinitesimally thin annulus at a given distance,  $r$ , can be estimated as:

$$p(r) = \frac{1}{2a\sqrt{2\pi r}} \exp\left[-\frac{(\ln r - \ln b)^2}{2a^2}\right] + \frac{1}{c\sqrt{2\pi}} \exp\left(-\frac{r^2}{2c^2}\right), \quad (4)$$

where  $a$  and  $b$  are empirically determined constants, and  $c$  is a linear function of the mean depth-averaged current speed over the dispersal period (Table 1) (Gaylord et al., 2006). This formulation possesses the fat-tailed character that is crucial for properly representing longer-distance portions of the dispersal distribution (Fig. 3), and can be recognized as the sum of a lognormal and normal probability density function, each scaled to ensure that their combination integrates to 1. Eqn 4 is a phenomenological representation of a more complex model that considers a suite of physical processes, including vertical mixing influenced by nonlinear wave–current interaction, oscillatory wave motions, and transport due to quasi-steady currents. However, its closed-form

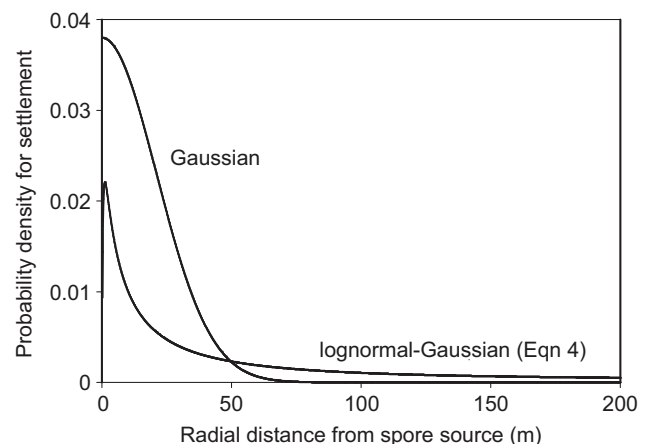


Fig. 3. Probability density function for spore settlement as a function of radial distance from a source kelp, assuming a lognormal-Gaussian dispersal distribution (parameters in Eqn 4 are  $a=1.78$ ,  $b=25$ ,  $c=1800$ ). Note the extended ‘fat tail’ of the distribution, which ensures appreciable amounts of settlement out to hundreds of meters. A one-sided Gaussian probability density function (which also integrates to 1.0 over positive distances) is shown for comparison. The Gaussian is parameterized so that the two curves match at a distance of 50 m (s.d.=21; this is an arbitrary choice used to highlight differences in the shapes of the tails).

nature enables it to be readily imported into spatially explicit metapopulation constructs. This feature provides a direct connection between first-principle hydrodynamics and quantitative ecological analyses, yielding a potential means of extending earlier non-spatial treatments (e.g. Nisbet and Bence, 1989) [see also Baskett (Baskett, 2012) for analogous examples of how links between mechanics and theoretical ecology can employed].

#### Spore production as an analogue to local births

Along with improved estimates of dispersal potential, recent work has facilitated the development of more accurate estimates of kelp fecundity, which relates to  $B$  in Eqn 1 (i.e. births). This information was acquired by comparing field measurements of densities of settled spores at multiple distances from source kelps with densities of spores predicted from coupled physical-biological dispersal models (Gaylord et al., 2006). By scaling predicted patterns of dispersal to observed patterns of settlement, rates of spore production in *Macrocystis* could be estimated. These analyses suggest tremendous rates of production and release: approximately 100 million spores per individual per day. These rates are consistent with expectations of high kelp fecundity based on artificial manipulations of individual reproductive blades (e.g. Anderson and North, 1966), but were determined using field data and may provide more realistic bounds on this core demographic parameter.

Note that the two-phase life cycle of kelps adds complexity when attempting to relate spore production to birth rates. In the present review, births are equated with spore release by an adult plant, which is when spores become freely living. An alternative approach would be to census births at the point of sporophyte establishment, which occurs after passage through the second life stage. The latter method is likely more appropriate when haploid/diploid distinctions are important. However, it is less easily merged with simple demographic analyses. For this reason, and to maintain analogy with marine invertebrate systems where larvae represent births, we count newly released spores as births. The creation of a sporophyte through fusion of sperm and egg (which proceeds only if spores of both sexes settle close together and the ensuing gametophytes survive) then operates as an additional density-dependent hurdle that arises subsequent to the birth, immigration and/or emigration steps.

#### Self-fertilization and inbreeding

Mechanistic predictions of spore production and dispersal also enhance understanding of the capacity for inbreeding in kelp forests, a phenomenon that can influence birth and death rates. Kelps are self-fertile, with fertilization occurring after dispersal, as noted previously. The leptokurtic shape of the dispersal distribution (Fig. 3) ensures that many spores will settle quite close to the adult, even as appreciable numbers travel large distances. If there are few other adults nearby that are also releasing spores, a large fraction of settling spores may be from the same parent. This situation increases the probability of selfing. Self-fertilization may be especially pronounced in isolated kelp patches or in forests characterized by larger but sparsely distributed individuals (Fig. 4). Denser forests that damp flows within their boundaries may also exhibit higher levels of inbreeding. Importantly, it appears that selfing costs are quite substantial and, at least in *Macrocystis*, can be manifested at multiple life stages (Raimondi et al., 2004). For instance, rates of successful zygote formation decline by 40%, resulting in fewer individuals reaching adulthood, and selfed adults exhibit dramatically lower reproductive capacity (reductions of nearly 90%). The ability of impacts on spore production (=reduced

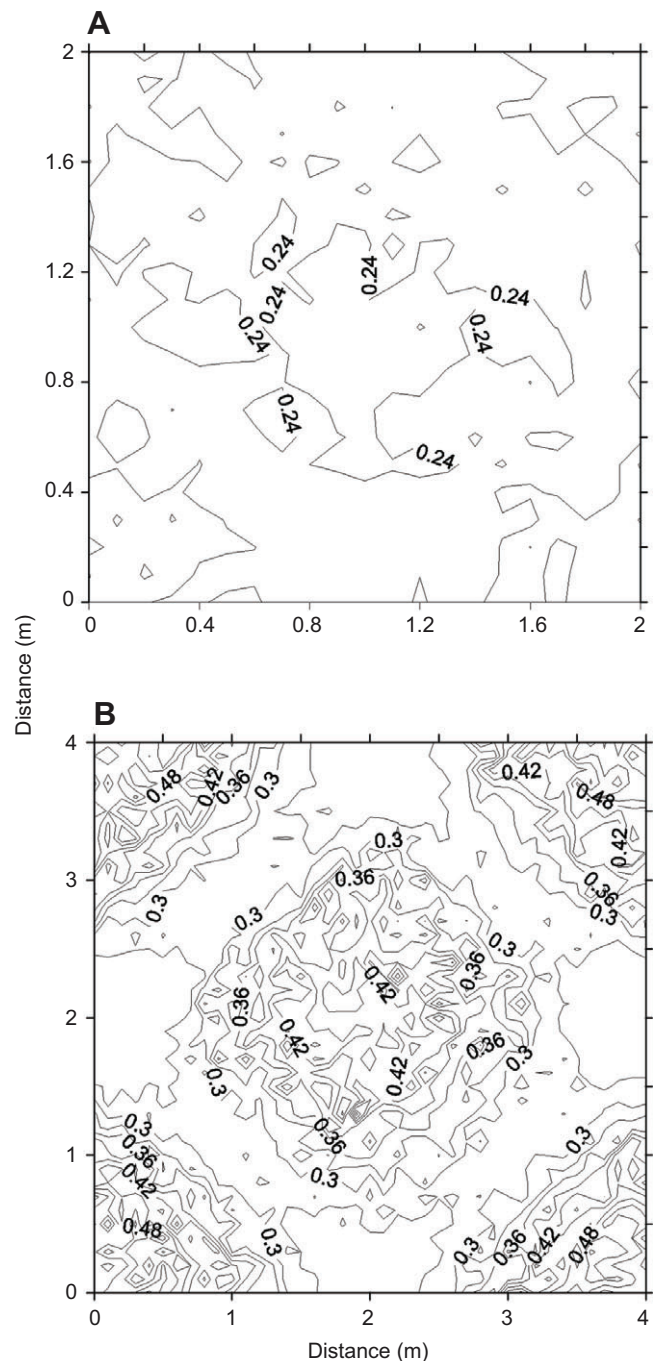


Fig. 4. Predicted probabilities of self-fertilization, depicted as proportions of 1.0, in an idealized sector of a kelp forest. Adults are assumed to be located in the center and at each corner of the sector. (A) Nearest-neighbor distances of 1.4 m. (B) Nearest-neighbor distances of 2.8 m [redrawn from Gaylord et al. (Gaylord et al., 2006)].

births), or losses at zygote and juvenile stages (=increased deaths), to contribute to commonly observed population fluctuations in kelp forests warrants further attention (Raimondi et al., 2004).

#### Genetic structure within and among forests

Dispersal and self-fertilization also influence genetic structure in kelp populations. Intriguingly, modern genetics methods largely affirm predictions based on ecomechanical approaches. For

example, they demonstrate that levels of oceanography-controlled population connectivity, as influenced by habitat continuity, provide a better prediction of genetic divergence among individuals drawn from multiple *Macrocystis* forests than simple straight-line or along-coast geographic distances (Alberto et al., 2010). Other research has revealed signatures of the strengths of boundary currents on patterns of connectivity (Coleman et al., 2011). Emerging genetic studies also verify asymmetric connectivity among populations due to preferential trajectories in current-driven transport (e.g. Alberto et al., 2011).

### Opportunities for progress

The value of mechanics-based approaches for addressing population questions in kelp forests is clear from their capacity to enhance understanding of dispersal and its impacts on birth, death, immigration and emigration rates. There are additional ways in which considerations of transport and mixing processes can inform kelp forest ecology as well. Below we identify topics in the dispersal sector, and in other sectors, that are worthy of further attention.

#### Improving dispersal and connectivity estimates

One limitation of existing dispersal representations (and thus estimates of  $I$  and  $E$  in particular) is that they have not typically accounted for the effects of kelps themselves on phases of spore transport taking place within a forest. This means that short-distance portions of the dispersal distribution may be subject to error. Until recently, this weakness was not easily addressed. Despite early work examining the ability of kelp forests to attenuate currents within their interior (Jackson and Winant, 1983; Jackson, 1998), there was little information available for generalizing to forests of a broader array of sizes, densities or geometries. Perhaps even more crucially, measurements of vertical mixing within forests were absent. However, several recent studies (Gaylord et al., 2007; Rosman et al., 2007; Rosman et al., 2010) have offset some of these challenges. Findings now suggest that a profitable approach could be to take phenomenological dispersal representations developed for within- and outside-forest portions of the spore transport process, and combine them. Each representation would be based on its own appropriate patterns of vertical mixing as quantified by Eqns 2 and 3. Data such as those presented in Fig. 2 could also be employed to estimate current velocities at various positions within a forest. Whether core conclusions would change with the addition of such complexity is unclear, but warrants evaluation.

There are also opportunities to incorporate individual-level variation in biological parameters (e.g. spore production and position within a forest) into population analyses. Dispersal distributions from multiple individuals could be summed to provide quantitative approximations of spore output from an entire forest. Forests of different ages are often characterized by distinct size structure. For example, older forests may have more sparsely distributed but larger and more productive individuals than younger forests. Summing dispersal distributions from multiple individuals configured with different spacing and/or possessing different numbers of reproductive blades could reveal much about how such factors influence connectivity among forests. Other elaborations are also possible. Individuals growing at deeper depths may exhibit subtly different dispersal patterns compared with individuals in shallower locations because of distinct hydrodynamic conditions. The same point holds for kelps growing at interior *versus* edge locations. Whether individuals that inhabit particular places in a forest contribute disproportionately to between-forest connectivity

is unknown, however. Other model incarnations could account for stochastic variation in environmental or biological factors through time.

At scales involving multiple forests where questions of broader seascape connectivity are relevant, there is excellent potential for meshing dispersal models with aerial maps and satellite technologies (Cavanaugh et al., 2010). Such integration could help to more fully define spatial structure and temporal variation at regional scales. Although a modest level of prior work in this area has taken place (e.g. Dayton et al., 1984; Reed et al., 2006), the full potential of this integration has not yet been realized.

Efforts to understand dispersal relevant to specific kelp forests and/or networks of forests could be facilitated through the use of tactical numerical oceanographic models that provide detailed estimates of dispersal trajectories in particular regions and during specific time periods. The most widely used construct for predicting circulation patterns is the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams, 2005). Work using this framework has been applied with some success to the study of larval dispersal (e.g. Cowen et al., 2006; Mitarai et al., 2008). The challenges are different for kelp spores because their reduced time in the plankton places them under greater control of nearshore currents, which have traditionally not been well resolved in such models. However, there remains room both for refinement of the predictions of these models and for improving more conceptual treatments that intentionally simplify the complexity of ocean transport [e.g. advection-diffusion and random-flight models (Jackson and Strathmann, 1981; Gaylord and Gaines, 2000; Siegel et al., 2003)].

A particularly useful addition to existing representations of dispersal would be the incorporation of new data on the structure of nearshore currents, which are typically not incorporated into oceanographic models and have not yet been embedded in simpler constructs. Velocity measurements made over the innermost portion of the continental shelf (depths <25 m) indicate a repeatable pattern of attenuation of alongshore currents within a ~1–5 km-wide ‘coastal boundary layer’ (Nickols et al., in review). Currents within this region exhibit characteristics analogous to those of smaller-scale (millimeter to meter scale) turbulent boundary layers. In particular, cross-shore gradients in depth-averaged alongshore velocity reproduce the canonical logarithmic profile commonly observed in many other types of flows (Fig. 5). This remarkable consistency could be incorporated into simple theoretical population models, and could have important implications (White et al., 2010; Nickols et al., in review). For example, it is possible that spores released from adult kelps on the offshore side of a forest could be entrained into faster currents than those released from the inshore side, elevating the degree of kurtosis in the dispersal distribution and altering patterns of population connectivity. An accompanying consequence of logarithmic coastal boundary layers is that kelp forests embedded in such flows will not only experience strong gradients in average alongshore current speed, but will also be subject to marked gradients in intensities of lateral mixing, which could influence transport trajectories of spores moving between and among forests.

#### Metapopulation elaborations

Quantitative representations of spore dispersal also provide opportunities to evaluate broader elements of demographic exchange among the forests comprising a kelp metapopulation. The frequency and severity of episodic perturbations of forests appear to be increasing in conjunction with atmospheric shifts tied to climate change or oceanographic regime shifts (e.g. Graham and

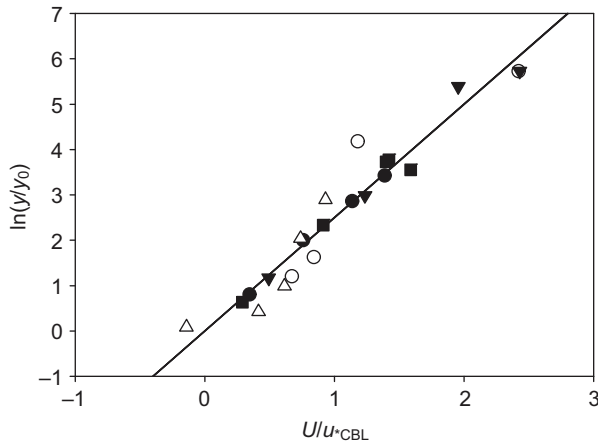


Fig. 5. Consistent logarithmic profiles of alongshore current speed observed within coastal boundary layers (CBLs) at five inner-shelf locations off the coast of California. If the distance from shore ( $y$ ; m) is normalized by a site-specific coastal roughness parameter ( $y_0$ ; m) and the mean depth-averaged alongshore current velocity ( $U$ ;  $\text{m s}^{-1}$ ) is normalized by a coastal shear velocity, ( $u_{\text{CBL}}$ ;  $\text{m s}^{-1}$ ), all the profiles collapse to a single line. This oceanographic pattern is analogous in general character to the law of the wall (Middleton and Southward, 1984), which applies to smaller-scale turbulent boundary layers. Various symbols correspond to velocity measurements from different locations [redrawn from Nickols et al. (Nickols et al., in review)].

Diaz, 2001; Bromirski et al., 2003; Parnell et al., 2010; Ruggiero et al., 2010). Therefore, rates of extinction of individual forests might be expected to increase. Any ensuing reduction in the fraction of kelp-suitable reefs that are occupied could have widespread repercussions, given that canopy-forming kelps are foundation species that provide biogenic habitat and food for hundreds of other taxa.

At present, potential responses of kelp metapopulations to altered extinction rates of their constituent forests are not well understood. Simple models predict qualitatively different regional outcomes in the face of altered local extinction risk, depending on how recolonization proceeds (Levins, 1969; Hanksi and Gilpin, 1991; Gotelli, 2001). Consider two illustrative constructs. The first is a situation where a particularly large and stable forest dominates regional spore production such that recolonization events across the entire metapopulation arise by means of a ‘propagule rain’. Then, the equilibrium proportion,  $f$ , of all kelp-suitable reefs that at any given time maintain viable populations is predicted to be:

$$f = \frac{p_i}{p_i + p_e}, \quad (5)$$

where  $p_i$  is the probability that an individual forest will be recolonized and  $p_e$  is the extinction probability for an individual forest. Of note is the nonlinear decrease in the fraction of kelp-suitable reefs supporting viable forests as  $p_e$  rises, which prevents  $f$  from reaching zero even if the local extinction risk is large. Next visualize a second, contrasting situation, where recolonization arises from spores released evenly from forests throughout the metapopulation. In this case, the equilibrium fraction of kelp-suitable reefs that maintain viable populations is predicted to be:

$$f = 1 - \frac{p_e}{i}, \quad (6)$$

where  $i$  is a parameter quantifying how the probability of recolonization increases with the fraction of reefs occupied by

forests (Gotelli, 2001). In this latter situation, there is a linear response to changes in local extinction rate, and if the extinction probability rises to where  $p_e = i$ , the fraction of reefs supporting kelp goes identically to zero. As a consequence, there is no built-in safeguard against regional extinction.

With the two scenarios of Eqns 5 and 6 providing conceptual scaffolding, mechanistically based dispersal distributions (Eqn 4) could be used to predict how strongly rates of spore delivery might decline with reductions in the number of extant forests. In particular, dispersal distributions from kelps in multiple forests could be superposed to determine how settlement densities of spores might depend on forest number, under the assumption that spore densities correlate with recolonization probability. If spore densities are predicted to decline strongly with reductions in forest number, this situation could imply that internal connectivity is crucial, and that a metapopulation might be vulnerable to overall extinction if local disturbance rates exceeded some threshold. In contrast, if spore densities appear relatively insensitive to reductions in the number of contributing forests, this situation could imply that a propagule rain scenario is more applicable, which in turn suggests a substantially reduced risk of plummeting kelp cover or overall extinction.

#### Nutrient delivery to forests

Transport and mixing processes control delivery of waterborne constituents beyond just spores to and from kelp forests. A number of these constituents have the capacity to influence kelp birth and death rates. It is well recognized that nutrient limitation acts as a major source of senescence and mortality in southern California populations of *Macrocystis* (Jackson, 1977). During El Niño events characterized by low seawater nitrate concentrations, there can be large die-offs (Tegner and Dayton, 1987), and nutrient delivery to forests can directly influence longevity of kelp individuals (Zimmerman and Kremer, 1984). Spontaneous recruitment engendered by activation of microscopic spore or gametophyte resting stages may also occur under conditions of higher nitrate concentrations (Carney and Edwards, 2010). It is known that a variety of transport processes, in particular those tied to internal waves, but also phenomena associated with mesoscale mixing, upwelling and general movement of the thermocline, can all modify rates of delivery of nitrate to kelp forests, particularly in deeper parts of the water column (Jackson, 1984; Leichter et al., 1998; Bassin et al., 2005; Rosman et al., 2007; McPhee-Shaw et al., 2007). Rates of larger-scale delivery can also interact with other components of water motion, such as tidal currents and waves, to influence kelp growth (Koehl and Alberte, 1988; Hepburn et al., 2007; Stewart et al., 2009) and potentially spore production. However, attempts to rigorously link delivery to utilization within a physically based framework are rare (e.g. Fram et al., 2008), and no study has directly embedded the governing physics into a quantitative population ecology analysis.

#### Linking transport and mixing to other physical processes

Although we have deliberately limited the scope of our discussion to transport and mixing phenomena, the processes we highlight are neither exclusive nor exhaustive. There are many other physical and biological factors that participate in controlling the population rate parameters of Eqn 1 (i.e.  $B$ ,  $D$ ,  $I$  and  $E$ ). A number of these additional processes interact with ones outlined above, and a subset exhibit clear potential for mechanics-based attention.

Consider two classes of factors that are known to influence kelp population dynamics. Focus first on forest-wide agents of physical

disturbance, which have a long history of attention (e.g. Dayton et al., 1984; Dayton et al., 1992; Dayton et al., 1999). Particularly amenable to physically based study are the effects of large waves produced during storms, which remove many individuals (Seymour et al., 1989; Graham et al., 1997). Although the basic cause-and-effect relationship between waves and kelp dislodgment is clear, there is unrealized potential for developing predictive relationships that link the fundamentals of hydrodynamic force imposition to population consequences (e.g. death rates). Efforts to simultaneously account for multiple physical processes would also be valuable, given what is known about recovery trajectories and factors influencing recolonization. For example, although waves can determine which and how many adults are removed, such losses also alter the canopy cover and thereby the amount of light reaching the understory, as well as levels of vegetation-mediated flow attenuation. Recruitment is known to depend strongly on competition for space and light (Deysner and Dean, 1984; Reed and Foster, 1984), and on the ability of settled spores to adhere under rapid flows (Taylor and Schiel, 2003).

A second example provides a reminder that biological and physical factors cannot always be partitioned cleanly. Biological pressures tied to grazing by sea urchins operate as a major source of kelp mortality, and changes in these pressures can cause forests to transition abruptly between algal- or urchin-dominated states (Pearse and Hines, 1979; Dean et al., 1984; Harrold and Reed, 1985; Ebeling et al., 1985). Most research has addressed the grazing-induced switch to the non-algal, barren state. However, anecdotal information also suggests that the transition of denuded forests back to a kelp-abundant state can be facilitated by the removal of urchins by storms (Harris et al., 1984). Such observational associations would benefit from mechanistic approaches that define thresholds of vulnerability of kelps and urchins to flow-driven disturbance. For example, although adult *Macrocystis* are removed routinely by seasonal storms, the degree to which more extreme storms might be required to impact urchins remains unclear. Quantification of such physical-biological interactions could contribute substantially to understanding nonlinear dynamics in kelp forest systems.

#### Connecting to community and ecosystem issues

Our discussions of how ecomechanics can inform kelp forest ecology have targeted largely population-level issues, where explicit connections between transport/mixing phenomena and ecological processes exist, and where some progress has been made. However, similar approaches could also be used to advance community- and ecosystem-level understanding. Consider for instance the recent controversy concerning the relative importance of top-down *versus* bottom-up control of kelp systems (Halpern et al., 2006; Foster et al., 2006). Such debates would benefit from more detailed consideration of subsidy inputs and exports, including those tied to nutrient supply and sloughing of blade tissue, as well as improved incorporation of physical processes at other levels. In a similar vein, the increasingly common use of structural equation modeling (e.g. Byrnes et al., 2011), which represents links among community elements in terms of quantitative expressions, could be enhanced by more accurate representation of those links based on physical, mechanistic principles.

There are many opportunities to undertake such refinements. Because it is known how kelp forests interact with impinging currents to alter intensities of transport and mixing, flow characteristics and feedbacks between water motion, forest

dimensions and community interactions can be addressed explicitly. As just one example, attenuated currents within forests may differentially affect suspension feeders living at various locations (i.e. forest interior or edge), including those that are epibionts on kelp, whose success feeds back to influence that of the macroalgae (Arkema, 2009). In other cases, direct and indirect interactions among species may be altered according to situation-dependent effects of kelp on a spectrum of environmental parameters (Fig. 6) (Arkema et al., 2009).

Considerable value could also accrue from comparative methods that take advantage of distinct characteristics of different canopy-forming kelp species, some of which can be co-located in space. Examples include the annual kelp *Nereocystis luetkeana*, which forms forests similar to those of the perennial *Macrocystis*, but which has its own unique features. For instance, it exhibits different patterns of spore release, an altered susceptibility to storm-driven mortality, distinct patterns of carbon and nutrient inputs/exports, and its own associated community of residents (Springer et al., 2010). Each of these differences could create species-specific interactions with transport and mixing phenomena or, for that matter, with fluid-dynamic processes more generally.

At the level of ecosystems, the movement of kelp material between and among habitats has been insufficiently explored.

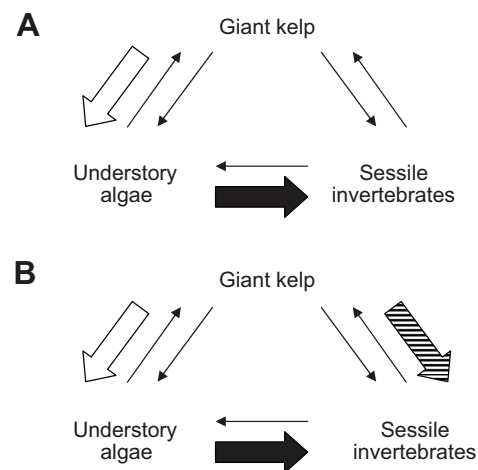


Fig. 6. Example set of species interactions in a kelp forest where mechanistic attention to transport and mixing phenomena could provide insight. Giant kelp, understory macroalgae and sessile invertebrates all compete for primary space on the seafloor, inducing both weak (thin black arrows) and strong (black block arrow, reflecting the tendency for algal overgrowth of invertebrates) direct negative effects on one another. Giant kelp also shades regions beneath its canopy, imposing a strong negative effect on understory algae through light limitation (open block arrow). The net indirect effect of giant kelp on invertebrates, ensuing from the summed consequences of the direct negative interactions, is therefore strongly positive. That is, the strong negative effect of giant kelp on understory algae removes the latter's ability to impede invertebrates, resulting in a strong net benefit for the invertebrates. (A) Situation in a kelp forest of modest size and density, where the above relationships adequately encapsulate the key competitive interactions [modeled after Arkema et al. (Arkema et al., 2009)]. (B) Hypothetical situation in a large or dense forest characterized by marked velocity attenuation. In this case, reduced intensities of transport and mixing could impair delivery of suspended food to invertebrates, introducing an additional, negative interaction into the system (hatched block arrow). Overall effects of giant kelp on sessile invertebrates could then become dependent on the relative magnitudes of the opposing strong interactions (i.e. the direct negative hydrodynamic impact *versus* the indirect positive impact transduced through the understory macroalgae).



Stable isotope methods have revealed the trophic importance of macroalgae in nearshore and even pelagic food webs (Dunton and Schell, 1987; Duggins et al., 1989; Fredriksen, 2003; Kaehler et al., 2000; Tallis, 2009), but these methods have not been able to resolve pathways of exchange. A mechanics-based approach that considers concentration gradients and patterns of transport of spores, exudate and small-scale particulates would be particularly useful to clarify processes of kelp-derived carbon delivery to benthic consumers, both inside and outside kelp forests. Such inputs of macroalgae are known to affect the ecology of nearby sandy shore (Dugan et al., 2003), terrestrial (Polis and Hurd, 1994) and deep-sea habitats (Harrold et al., 1998; Vetter and Dayton, 1999; Britton-Simmons et al., 2009). Examining the interplay of transport and mixing processes with kelp demographics and the time course of tissue production/degradation could help uncover patterns of resource delivery to these ecosystems. In this regard, such explorations could quantify a crucial factor controlling trophic dynamics in a suite of coastal environments, in particular, recipient habitats with low internal productivity.

### Conclusions

There is a long tradition in ecology of developing conceptually attractive, often quite simple representations of processes governing species distributions and abundances [i.e. keystone and foundation species concepts, intermediate disturbance and stress gradient hypotheses, reviews of the importance of facilitation, and so on (see Bertness et al., 2001)]. However, despite the obvious power of such broad-strokes models and their impressive legacies, they cannot explain all features of note. They also are rarely capable of making quantitatively accurate predictions about future dynamics or structure. It is in such instances where procedures for scaling up from physics-based principles and organism–environment interactions have considerable value. Ecomechanics provides one as-of-yet underutilized tool for undertaking such cross-scale integration, as evidenced by its application to kelp forests and the physical factors that operate within and around them.

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