

Wave energy and intertidal productivity

(leaf area index/*Mytilus californianus*/*Postelsia*/rocky shore/zonation)

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ABSTRACT In the northeastern Pacific, intertidal zones of the most wave-beaten shores receive more energy from breaking waves than from the sun. Despite severe mortality from winter storms, communities at some wave-beaten sites produce an extraordinary quantity of dry matter per unit area of shore per year. At wave-beaten sites of Tatoosh Island, WA, sea palms, *Postelsia palmaeformis*, can produce >10 kg of dry matter, or 1.5×10^8 J, per m^2 in a good year. Extraordinarily productive organisms such as *Postelsia* are restricted to wave-beaten sites. Intertidal organisms cannot transform wave energy into chemical energy, as photosynthetic plants transform solar energy, nor can intertidal organisms “harness” wave energy. Nonetheless, wave energy enhances the productivity of intertidal organisms. On exposed shores, waves increase the capacity of resident algae to acquire nutrients and use sunlight, augment the competitive ability of productive organisms, and protect intertidal residents by knocking away their enemies or preventing them from feeding.

Anyone who has felt the force of a large wave breaking on an ocean beach knows that it dissipates a large amount of energy when it crashes against the shore. Can intertidal organisms put this energy to use?

Water motion does enhance the growth of aquatic organisms. In general, productivity of marine and freshwater plants is higher in moving than in still water (1, 2). It has long been known that coral reef growth is most vigorous on those margins of the reef where waves pound hardest (3): indeed, wave-beaten reef platforms produce four times as much calcium carbonate per square meter per year as do those in protected lagoons (4). Increased exposure to waves does not always increase productivity. Along the southern coast of Chile, the subtidal kelp *Macrocystis* appears to grow best at intermediate levels of water motion: at the most exposed sites, storm waves tear these kelps away (5). On the rocky shore of Nova Scotia, *Laminaria longicuris* grow less rapidly, and stands of this kelp are less productive at a site fully exposed to ocean waves than at a more sheltered locale (6). In the northeastern Pacific, however, intertidal kelps do grow better in wave-beaten places, even though waves select stringently for small size (7), because winter storms shred the fronds of most kelps, and tear away many kelps and mussels (7–9). On Tatoosh Island, WA, the stipeless kelp *Hedophyllum* recovers from removal experiments within a year (10), whereas on the more sheltered shores of the San Juan Islands, recovery is less than half complete after 3 years (11). In general, intertidal zones of the northeastern Pacific are more completely covered by plants and animals the more exposed they are to wave action (table 1 of ref. 12).

In this report, we first calculate the energy supplied by waves to exposed shores of the northeastern Pacific. Next,

we estimate standing crop and productivity in different zones of exposed and sheltered rocky shores of Tatoosh Island (48° 19' N, 124° 40' W), showing that intertidal productivity is much higher in wave-beaten settings. Finally, we consider the various roles waves may play in enhancing the productivity of intertidal organisms.

METHODS

The Power Supplied by Breaking Waves. Calculating the power carried by waves in the open ocean. Waves generated anywhere in the ocean dissipate most of their energy against some shore as surf (13, 14). To calculate the energy transported by waves in the open ocean, we assume that an indefinite train of sinusoidal waves transports an amount $P = (\rho G^2/4\pi)VT$ of energy per second per centimeter width of wave crest, across an imaginary plane perpendicular to the direction of motion of the waves: here, ρ is water density, assumed to be 1 g/cm³; G is gravitational acceleration, assumed to be 10^3 cm/sec²; V is variance in water level, in cm²; and T is wave period, in seconds (ref. 14, section 3.4). For a superposition of sine waves all moving in the same direction, T is the average of the various wave periods, weighted according to the contribution to V of the waves in question.

We have calculated P , which we call wave power, for three sites: Gray's Harbor, WA (46° 47' N, 124° 50' W), a wave buoy 5 km seaward of Tofino, British Columbia (49° 9' N, 129° 54' W), and Cobb Seamount (46° 45' N, 130° 50' W), 500 km west of Gray's Harbor. The calculations for Gray's Harbor are based on daily records of V , called “wave energy,” and of the proportions of this wave energy contributed by waves of different periods, provided by the Near-shore Research Group, Institute of Marine Sciences, Scripps Institution of Oceanography, La Jolla, CA. The calculations for Tofino are based on monthly tables (15) of “significant wave height,” $4V^{1/2}$, as distributed over various wave periods. Larsen and Fenton (16) provide daily records of root-mean-square wave height, $(8V)^{1/2}$, and wave period, for Cobb Seamount.

We compute wave power as if all waves are moving in the same direction, toward the coast. As we shall see (Table 1), the wave power calculated for the two nearshore stations is comparable to that calculated for Cobb Seamount, as if most of this power is directed eastward or northeastward toward the shores of Washington state and Vancouver Island.

The power delivered by waves to the intertidal zone. On steep shores, such as the western shore of Tatoosh Island, waves break in the intertidal zone, dissipating most of their energy there (7, 17). Some wave energy may be reflected back out to sea (18), but organisms on the reflecting surface presumably could benefit from this energy. To calculate the energy that waves deliver to the intertidal zone (including the energy reflected as well as that which is dissipated), we

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Abbreviations: MLLW, mean lower low water; FAI, frond area index; LAI, leaf area index.

Table 1. Energy transported per centimeter of wave crest per second (W/cm) at selected sites: monthly averages

Month	5 km seaward from Tofino, British Columbia (49° 9' N, 129° 54' W)					Cobb Seamount (46° 45' N, 130° 50' W)	Gray's Harbor, WA (46° 47' N, 124° 50' W)
	1969–1970	1970–1971	1971–1972	1972–1973	1973–1974	1972–1973	1982
September			188		142	109	
October			268		297	280	559
November			611		439	887	400
December			435		636	728	775
January					774	711	698
February			213	322	577	506	383
March				468	498	836	430
April		324	243	217	222	263	251
May		259	109	151	201		165
June			105	205	163		
July	109	46	71		100		
August	84	113			75		

Energy is calculated as if all of the waves are moving in the same direction. The data are taken from the sources listed in *Methods*.

assume that the ocean waves offshore are all moving directly shoreward and that their power is delivered to an "intertidal zone" extending from the upper limit of barnacle settlement down to mean lower low water (MLLW). MLLW is the average of observed water levels at times listed in National Oceanographic and Atmospheric Administration tide tables for the lower of the two daily low tides. On the most exposed shores at Tatoosh, this intertidal zone is roughly 5 m deep (Table 2). Finally, we assume that the shore is inclined at an average of 30° to the horizontal, so that the intertidal zone is a strip 10 m wide and that wave power is distributed evenly over this strip.

These calculations are clearly very crude. Not all of the energy in ocean waves reaches the shore. Moreover, power is not distributed evenly over the intertidal zone. On the southwest side of Tatoosh, wave force is strongest just above the mussel zone (18), 2.75 m above MLLW. Finally, during storms, much of the wave power is dissipated above the intertidal zone. Our crude calculations, however, give some idea of the power supplied by breaking waves.

Relationship Between Productivity and Wave Power. To explore the relationship between wave power and intertidal productivity, we assessed zonation at various sites on Tatoosh, exposed and sheltered. At these sites we also measured standing crop, as dry matter and as combustible energy, per square meter of substratum; the frond area index [(FAI) one-sided frond area per unit area of substratum]; and the annual production of dry matter and energy per unit area.

Since, for a given tidal regime, the vertical extent of the intertidal zone is greater the more exposed that zone is to the waves (19), we measured the degree of exposure to ocean waves by the vertical extent of the intertidal zone—that is, the height from MLLW to the top of the *Balanus glandula* zone (the upper limit of perennial sessile animals).

We assessed zonation by recording the upper and lower limits, relative to MLLW, of common algae and sessile invertebrates. Each upper and each lower limit is the average of five or more readings taken with a transit and surveyor's rod.

We measured standing crops of the different algae on Tatoosh, usually in the late spring or early summer of several different years, at sites where it was relatively luxuriant. We cleared algae from plots of known area and weighed the harvest wet, except for one *Lessoniopsis* measurement. To convert from fresh wet weight to dry weight and energy content, we measured the dry matter content of *Iridaea cornucopiae* (22%), *Lessoniopsis* fronds (18%), and *Postelsia* fronds (13%) and stipes (9%), according to the methods of Paine and Vadas (20). We assumed that the energy content of dry *Iridaea cornucopiae* was the value given in ref. 20 for *Gigartina papillata* and that the energy content of dried *Lessoniopsis* fronds was the July 1971 value (2.8 kcal, or 11.7 kJ, per g of dry weight) in ref. 21. Dry matter and energy contents of other algae were taken from ref. 20.

We estimated frond area per unit weight for each alga in one or more harvests by laying out a known weight, usually very nearly the whole harvest, of suitably cut fronds on a flat surface, arranging them to form a rectangle with minimal gaps and overlap, and dividing the area of that rectangle by the fresh weight of the fronds therein to get frond area per unit weight. Values obtained in different harvests of the same alga rarely differed by >10%. We used the average of these values for a given species to calculate frond area from frond weight in other harvests of that species where frond area was not measured directly. FAI, the marine analogue of the forester's leaf area index (LAI), is (one-sided) frond area per kg of fresh weight, multiplied by kg of fresh weight of fronds per m² of substratum.

Table 2. Vertical distances (m) above MLLW of upper and lower limits of representative species at four intertidal sites on Tatoosh

Species	Site 17	Site 16	Simon's Landing	Strawberry Draw	Pole Island Draw
<i>Balanus glandula</i>	5.4–3.4	5.2–2.9	3.5–2.0	2.8–1.5	2.3–1.7
<i>Iridaea cornucopiae</i>	4.6–2.9	4.2–3.0	2.9–2.2	None	None
<i>Postelsia palmaeformis</i>	3.1–1.5	3.3–0.9	None	None	None
<i>Fucus distichus</i>	None	None	2.7–2.0	1.9–0.6	2.0–0.7
<i>Mytilus californianus</i>	3.1–0.6	3.0–0.7	2.7–0.9	1.7–0.8	1.3–0.6
<i>Hedophyllum sessile</i>	None	None	1.4–0.1	1.1–0.1	0.3–0.0
<i>Lessoniopsis littoralis</i>	1.0	1.0	0.5	None	None
<i>Laminaria setchellii</i>	–0.1	–0.1	–0.1	–0.4	No data

Each upper and lower limit is the average of five or more readings taken with a transit and surveyor's rod. MLLW is assumed to be the average of observed water levels at times listed for the lower of the two daily low tides in National Oceanographic and Atmospheric Administration tide tables.

We calculated algal productivity by multiplying frond weight per unit area by the number of times the fronds were replaced per year and, for the annual kelp *Postelsia* (22), adding the stipe weight per unit area to this product. J.F.Q. measured the number of frond replacements per year by punching holes at the bases of selected fronds (23), summing the lengths these fronds would have attained during the growing season in the absence of wear, as judged by the rates at which these holes move outward from the bases of these fronds, and dividing by the sum of the observed maximum lengths of these fronds. Quinn finds a minimum of three replacements per year in *Postelsia* and *Lessoniopsis*, at both Tatoosh and Bodega Head, CA (38° 18' N, 123° 3' W); we assume one replacement per year in *Hedophyllum*.

We also estimated the standing crops and productivity of mussel beds. Suchanek (24) harvested 30 × 30 cm plots of mussels from different tidal levels at Tatoosh and measured the shell length of each mussel; one of us (R.T.P.) did likewise for a plot of comparable size at one of the most wave-beaten shores of Tatoosh. From data graphed on p. 58 of ref. 24, we find that \log_{10} (fresh flesh weight of mussel, g) = 2.6692 \log_{10} (shell length, mm) - $\log_{10} 11,073$ ($r^2 = 0.9691$, $n = 44$) and that 20.2% of the flesh weight of mussels 61–80 mm long, 22.9% in those 81–90 mm long, 26.8% in those 91–110 mm long, and 36.8% in mussels >110 mm long is gonad. If we assume that the dry matter and energy content of the flesh of *Mytilus californianus* are identical to those given for the South African mussel *Aulacomya* in ref. 25, the regression allows us to calculate the standing crop of mussel flesh and of mussel gonad harvested from our sample plots. Table 3 omits standing crops for recently disturbed sites.

We calculate a mussel stand's productivity as (1/8) (standing crop of mussel flesh) plus (1/2) (standing crop of mussel gonad), since *Mytilus californianus* spawn out half their gonad each year (32), while mussel beds are cleared once every 8–10 years, and only begin rebuilding 2 years after clearance, so that a mature mussel bed represents ≈8 years' growth (8).

RESULTS AND DISCUSSION

The Power Supplied by Breaking Waves. If we assume that all of the energy of ocean waves is delivered to the intertidal

zones of shores facing the waves, then such shores would receive an average of 325–350 W/cm of coastline (Table 1), or 13–14 horsepower per foot of shore. Such wave power may not be unusual: Munk and Sargent (33) computed that shores of Bikini Atoll facing the prevailing trade winds received an annual average of 8 horsepower per foot of shore (200 W/cm) from ocean waves.

Three hundred watts delivered over a 1-cm strip extending across an intertidal zone 10 m wide, such as that on the west side of Tatoosh, is 0.3 W/cm². During the calmest month recorded in Table 1, waves delivered 45 W/cm to exposed shores near Tofino, British Columbia: this amounts to 0.045 W/cm² for an intertidal zone 10 m wide. By contrast, in the sunniest month of the year, solar radiation in the northeastern Pacific averages between 0.017 and 0.025 W/cm² of land surface (table 25, p. 103 of ref. 34). In effect, intertidal zones of rocky weather coasts collect an extraordinary amount of mechanical energy, concentrating it from a wide area.

Relation Between Productivity and Wave Power. If we measure the degree of exposure to ocean waves of various sites at Tatoosh by the depth of the intertidal zone at these sites, we find that organisms that maintain the highest standing crops of organic matter—lower intertidal mussels, sea palms (*Postelsia*), and shrubby kelps (*Lessoniopsis*)—are restricted to the most wave-beaten areas. These standing crops are, nonetheless, far lower than those to which forest ecologists are accustomed (Table 3). The situation is quite different for frond area. The *Lessoniopsis* we sampled maintained 15–24 m² of fronds (counting one side only) per m² of substratum. Tropical rain forest, that most luxuriant of broadleaf forests, probably maintains little more than 8 m² of leaves per m² of ground, although higher values have been reported (35). Coniferous forests have been reported with as many as 19 m² of leaves (again, one-sided) per m² of ground (36), but these leaf areas were inferred from tree diameters by allometric relations of a sort likely to lead to overestimates (35, 36). In any event, the frond areas of algae restricted to the wave-beaten sides of Tatoosh often far exceed the leaf areas of broadleaf forest, and the frond areas in our most luxuriant stands of *Postelsia* and *Lessoniopsis* are extraordinarily high by any standard.

Moreover, the two algae, *Postelsia* and *Lessoniopsis*, that grow only on wave-beaten shores are the most productive

Table 3. Range of standing crop, productivity, and FAI (LAI) for single-species stands at Tatoosh and for selected forests

Sample	Number of samples	Harvest plot size, m ²	Productivity		Standing crop		FAI
			Dry matter, kg/m ² per year	Energy, J/mm ² per year	Dry matter, kg/m ²	Energy, J/mm ²	
Intertidal species (Tatoosh)							
<i>Iridaea cornucopiae</i>	4	0.02–0.09	No data	No data	0.7–1.0	10–14	6–7
<i>Postelsia palmaeformis</i>	10	0.25	3.8–14.6	57–217	2.0–7.3	30–108	8–34
<i>Fucus distichus</i>	4	0.16–0.25	No data	No data	1.4–1.6	20–23	6
<i>Mytilus californianus</i>							
Upper	5	0.09	0.2–0.3	3.8–6.7	1.3–2.1	29–47	
Middle	4	0.09	0.7–1.2	16–26	3.1–5.6	69–124	
Lower	3	0.09	1.6–1.9	36–42	5.4–6.5	120–144	
<i>Hedophyllum sessile</i>	5	0.5–1.0	1.4–2.7	16–32	1.4–2.7	16–32	5–8
<i>Lessoniopsis littoralis</i>	3	0.69–2.4	6.9–8.6	81–101	4.0–4.6	47–54	15–24
<i>Laminaria setchellii</i>	4	0.5–1.0	1.6–3.3	18–39	3.3–6.8	39–81	5–12
Forest							
Rainforest							
Pasoh, Malaysia	1	8 × 10 ³	2.7	45	43	720	8
Côte d'Ivoire	1	8 × 10 ²	1.7	28	56	939	10–12
French Guiana	1	Not given	1.2	20	32	531	No data
Douglas fir, Oregon	1	About 10 ⁴	1.3	22	117	1952	13

Energy content of the forest communities is calculated assuming 4 kcal, or 16.7 kJ, per g of dry weight (see table 23 in ref. 26). Data for Malaysia and French Guiana are from refs. 27 and 28, respectively; data for the Côte d'Ivoire are those given for Banco in ref. 29, except for the LAI, which is from ref. 30; data for Oregon are for the *Pseudotsuga-Castanopsis* community in ref. 31.

algae at Tatoosh. Beds of these algae often produce >6 kg of dry matter per m² of substratum, twice as much as rain forests (Table 3). *Postelsia palmaeformis* produces up to 14.6 kg of dry matter per m² in a year: the highest terrestrial figures recorded in table 4 of ref. 37 are 8.5 kg/m² per year for a stand of the grass *Pennisetum purpureum* in Hawaii and 6.4 kg/m² per year for a Hawaiian field of sugar cane. Finally, those beds of mussels, *Mytilus californianus*, that are situated low in the intertidal zone produce as much dry matter—1.6–1.9 kg/m² per year—as some rain forests, even though mussels are consumers. The mussel bed, however, spreads this far down into the lower intertidal only at wave-beaten sites.

How Waves Enhance Intertidal Productivity. What permits such high productivity at wave-beaten sites? Organisms cannot transform wave energy directly into carbohydrates, as they do solar energy, nor do they “harness” it for other purposes, as a farmer’s windmill harnesses the energy of wind to pump water. Nevertheless, wave energy confers a variety of benefits on intertidal organisms.

(i) Waves aid in protecting intertidal inhabitants from their principal enemies (38, 39). In the northeastern Pacific, starfish, *Pisaster ochraceus*, normally restrict mussels to the upper and middle intertidal (40, 41), whereas sea urchins, *Strongylocentrotus purpuratus*, can destroy a kelp forest if unchecked (42), as can their counterparts, *Loxechinus*, in southern Chile (5). At Tatoosh, however, starfish will not feed in heavy wave surge, and at wave-beaten sites sea urchins are confined to clefts. In those areas of southern Chile where sea urchins destroy those kelp beds they can reach, kelps grow readily where waves protect them from urchins. Similarly, on Caribbean reef fronts where continual turbulence prevents parrotfish and the long-spined sea urchins, *Diadema*, from feeding, coralline algae grow readily, forming algal ridges; but these ridges decay if later reef growth, further out to sea, protects them from waves (43). On shores where waves predictably reduce the effects of herbivores, algae need invest less in chemical or structural defense and can channel more resources into growth (44). If, as we shall argue below, waves enhance algal productivity in other ways, optimal expenditure on chemical defenses will be even lower, for these conditions make it more profitable for algae to outgrow, rather than poison, their herbivores (44).

(ii) Waves strip away the boundary layer of used water from kelp blades, thus facilitating nutrient uptake. Wheeler’s (45) calculations and observations indicate that nutrient uptake by the fronds of the kelp *Macrocystis pyrifera* increases with the speed of water movement over the fronds, unless the water is moving faster than 5 cm/sec, at which point the rate of nutrient uptake levels off. Five centimeters per second is rather slow motion for water (ref. 46, p. 69): the average velocity of water motion must exceed 5 cm/sec all around Tatoosh. Nevertheless, kelps on the more sheltered sides of Tatoosh may well experience dangerously still water more often than their more wave-beaten counterparts, and the productivity of these sheltered kelps may be reduced accordingly.

(iii) Waves apparently enhance algal productivity by allowing algae to use light more efficiently. In broadleaf forest, each layer of leaves takes up roughly half the remaining light. In the rain forest at Pasoh, for example, 8 m² of leaves per m² of ground take up 99.5% of the incident light (27). If each layer is equally efficient, as figure 24.5 of ref. 27 appears to suggest, then each layer of leaves allows $(0.005)^{1/8}$, or 51.5%, of the remaining light to pass. Thus, while canopy leaves are receiving far more light than they can use (47), the herbs of the forest floor are receiving just enough light for their photosynthesis to earn them a meager profit (48). Similarly, a layer of *Macrocystis* fronds takes up two-thirds of the light reaching it (49). For various algae, the light level at which photosynthesis just balances respiration appears to be be-

tween 2 and 5 microeinsteins (μE) per square meter per second (50), compared to 4–10 $\mu\text{E}/\text{m}^2$ per sec for herbs on the floor of rain forest in Malaysia (51). Thus, if a kelp forest is to maintain a frond area per unit ground area much higher than that of a rain forest, as *Postelsia* and *Lessoniopsis* so clearly do, light must somehow be divided more evenly among their fronds than among the leaves of a forest. We believe that waves stir their fronds, ensuring that no frond is either always in the sun or always shaded. As photosynthesis of a leaf (and presumably that of a frond) in light fluctuating with a period between 0.01 and 100 sec is the same as that of a leaf subject to constant light of the same average intensity (57), stirring of the fronds by waves must cause light to be shared more evenly among the fronds, thus allowing the development of greater frond area. The influence of waves is particularly important because, especially in cold water (52), the photosynthesis of kelp blades and other algal fronds saturates at low light levels, achieving its maximum rate at 50–200 $\mu\text{E}/\text{m}^2$ per sec, 5–20% of full sunlight, although photosynthesis does not decline with a further increase of light (50, 52–54). Thus, a frond wastes light if it is exposed to the sun >5–20 sec of every 100. Leaves cannot possibly share the light so evenly in a rain forest, where a sunleaf of a canopy tree spends most of its time in full sunlight, while a forest floor herb receives sunflecks for only a few minutes per day. On the other hand, the shapes of the long, narrow, flexible fronds of *Postelsia* and *Lessoniopsis*, and their arrangement on the plant, make it possible for any of a plant’s fronds to be temporarily shaded or overtopped by nearly any other, and to be temporarily exposed to full sunlight soon thereafter, as long as the waves supply enough turbulent force to knock their fronds about. On Tatoosh, the restriction of algae with very high frond areas to wave-beaten sites suggests that waves do make it possible for these plants to maintain many fronds.

(iv) Waves enable some of the shore’s more productive inhabitants to displace their competitors. Waves permit the stiff-stiped kelp *Lessoniopsis* to flay or whiplash its competitors within a distance of roughly half a meter (11). Where mussels have settled around the kelps, the kelps are shredded against the sharp edges of the mussels, or crushed between them (12, 41). *Postelsia* lets the waves “compete on its behalf,” occupying gaps that waves clear from mussel beds (22, 55).

CONCLUDING REMARKS

In sum, shorelines exposed to ocean waves benefit from wave energy generated by winds anywhere in that ocean. As a result, the intertidal zones of rocky weather coasts receive far more energy from the waves than from the sun. Wave power enables the inhabitants of the weather coast of Tatoosh to maintain exceptionally high productivity, rather than the power that oil provides American farmers increases agricultural productivity by allowing crops to be fertilized and protected from pests and competing weeds, and by permitting feed to be concentrated so that great numbers of animals can grow and reproduce in one place (56).

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