



Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary

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ABSTRACT: Multiple stressors in estuaries can cause declines in native species and impairment of ecosystem goods and services. In contrast, one stressor—the introduction of non-native species—actually leads to higher local richness. We examined the changes in ecosystem function associated with introductions into Willapa Bay, Washington, USA, a relatively undeveloped estuary with 45 documented exotic marine species. The replacement of native oysters by 2 new bivalve species has increased secondary production of harvested suspension feeders by 250% over peak historic values (3.3×10^5 vs. 0.9×10^5 kg dry wt yr⁻¹), based on >150 yr of records of harvested biomass. Key aspects of aquaculture—particularly planted area—have remained constant over time, so we attribute much of the altered secondary production to higher growth rates of non-native species. The addition of 2 tracheophytes has increased primary production on the tideflats by >50% (5.3×10^7 vs. 3.5×10^7 kg dry wt yr⁻¹), which we calculated by scaling up local measurements of plant growth to the total area occupied by each species. These changes in production are also associated with altered detritus, water filtration, and biogenic habitat. Because other stressors are largely absent from Willapa Bay, the addition of particular exotic species has dramatically enhanced system production, while fundamentally reshaping the ecological character of the estuary. These strong ecological impacts of introduced species have rarely been measured at whole-ecosystem scales, and they occur in part because new species occupy habitats where similar native species were not present.

KEY WORDS: *Crassostrea gigas* · Invasion · *Ostreola conchaphila* · *Spartina alterniflora* · *Ruditapes philippinarum* · *Zostera marina* · *Zostera japonica*

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INTRODUCTION

Many recent studies reveal a saturating relationship between ecosystem functions and species richness, with marginal change attributable to additional species when many others are already present (Hooper et al. 2005). In contrast, the addition of species through ecological invasion can cause dramatic change. Ecosystem functions are expected to be altered by exotic species that play entirely new roles in ecosystems (Shea & Chesson 2002, Cuddington & Hastings 2004), and some empirical examples exist (e.g. *Myrica faya*

alters nutrient cycling in Hawaii where no native N-fixing plants occur; Vitousek & Walker 1989). However, to date, ecologists have been presented with few opportunities to study whole-ecosystem impacts of introduced species. For instance, Parker et al. (1999) found just 18 examples of ecosystem-level impacts of invaders reported over a 10 yr period, across all taxa and ecosystems, whereas impacts at individual, population, and community levels were studied more frequently (>90% of total). A unique opportunity arises in Willapa Bay, Washington, USA (46° 40' N, 124° 0' W; surface area at mean sea level = 24 000 ha), where

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lengthy time series and spatially explicit data allow reconstruction of primary production of tracheophytes and secondary production of bivalves over more than a century, during which period numerous nonindigenous species arrived. In this paper, we focus on 4 introduced species in Willapa Bay and document their contributions to primary and secondary production in the estuary. This case study illustrates 2 points: first, that gains in species—as much as species losses—can markedly influence whole-ecosystem functioning and therefore warrant the attention of predictive ecology and, second, that major changes in ecosystem functioning can be attributed to a few high-impact species rather than increases or decreases in numbers of species per se.

To set the stage for calculating whole-ecosystem changes and discussing their generality, we first present an ecological history of the bay. Willapa Bay is widely touted as pristine and productive (Wolf 1993, NOAA 1997), as it is largely unaffected by the pollution and coastal development that plague other estuaries. Chemical and nutrient pollution has historically been negligible, due to the sparse human population, minimal development in the watershed, and the absence of major industrial activities. About 30% of the 3500 ha of tidal marsh between mean high and extreme high water has been lost to diking for agriculture or expanding towns (Borde et al. 2003), but little other bathymetric modification has occurred since 1977 when maintenance dredging of the Willapa River channel ended (Hedgpeth & Obrebski 1981). Sediment loads to the bay have likely varied over the past century of logging within the watershed (Hedgpeth & Obrebski 1981, Kehoe 1982, Komar et al. 2004), and as a result of damming the Columbia River, the second largest river of the continental United States, which exits just south and often influences conditions at the bay's mouth (Simenstad et al. 1992, Peterson et al.

2000). The impacts of diking and sediment loading peaked by the mid-20th century and have since been constant or declined. The bay is also highly productive, as evidenced by its shellfish industry: although it is only $\frac{1}{30}$ the size of Chesapeake Bay on the east coast of the United States, nearly 10% of the United States' oysters are harvested there (US total = 16 804 metric tons shucked annually; Pritchard 2004), and shellfish production has contributed significantly to the local economy for >150 yr (Espy 1977). In contrast, over the same time period, oyster production on the east coast of the United States has dropped by >90% (Kirby 2004), in part due to habitat degradation.

While its physical and chemical changes have been minimal (therefore remaining relatively 'pristine'), Willapa Bay has been biologically transformed by introduced species (Fig. 1). The tally now stands at 45 new plants, algae, and invertebrates (Wonham & Carlton 2005), which comprise >10% of the total estuarine biota (Ferraro & Cole 2004). Two introduced taxa are particularly prominent: bivalve molluscs and aquatic tracheophyte plants. Pacific oysters *Crassostrea gigas* (Thunberg, 1793) were introduced to Willapa Bay in 1928 after native oysters *Ostreola conchaphila* (= *Ostrea lurida*) (Carpenter, 1857) were overexploited and transplants from eastern North America (*Crassostrea virginica* [Gmelin, 1791]) failed to thrive (Kincaid 1968). Early aquaculture activities involving these introduced oysters served as a vector for numerous other introductions (Carlton 1992).

The baseline bivalve community included thick accumulations of *Ostreola conchaphila*, covering up to 10% of the area of the bay, primarily in subtidal areas according to old charts (Collins 1892, Townsend 1896). *O. conchaphila* was commercially extinct by the early 20th century and, despite almost a century of low exploitation, remains rare in Willapa Bay (and throughout most of its range; Cook et al. 2000).

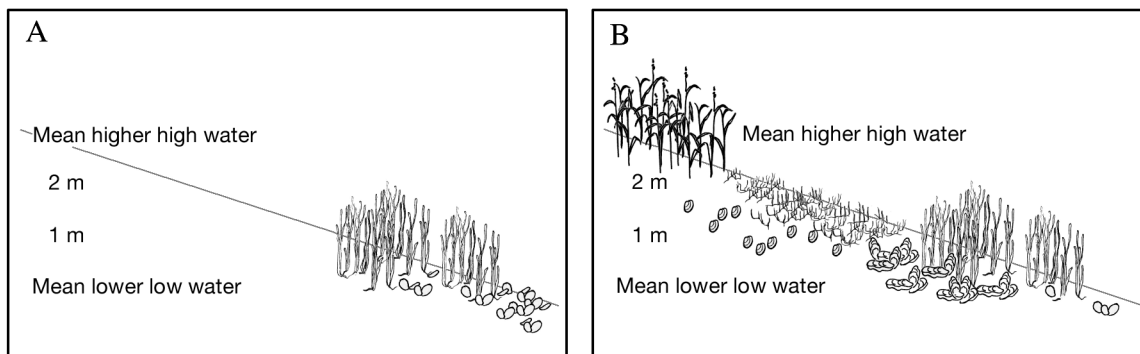


Fig. 1. Dominant space-occupying species on the tideflats of Willapa Bay. Vertical elevations (mean lower low water, 1 m above MLLW, 2 m above MLLW and mean higher high water) are provided to show where these species are found on tideflats. The slope of the tideflat (angled line) is exaggerated relative to field conditions. (A) Before 1900: native eelgrass *Zostera marina* and oysters *Ostreola conchaphila*. (B) After 2000: cordgrass *Spartina alterniflora*, Manila clams *Ruditapes philippinarum*, Japanese eelgrass *Zostera japonica*, and Pacific oysters *Crassostrea gigas*, in addition to native eelgrass and reduced densities of native oysters

The introduced oyster *Crassostrea gigas* constitutes the bulk of oysters currently harvested from the bay (at least 3 other introduced oysters are planted in small numbers) and occurs in 2 habitats. In upper portions of the estuary, it recruits reliably and forms dense intertidal hummocks (<1 to 100 m²) of tightly connected shell and live oysters. Many of these oysters are never harvested due to slow growth and irregular shapes. Nearer to the mouth, oysters are planted at relatively low densities directly on the bottom; oysters originate from natural recruitment elsewhere in the bay or from hatcheries.

A third bivalve, the Manila clam or Japanese little-neck *Ruditapes* (= *Venerupis* = *Tapes*) *philippinarum* (Adams & Reeve, 1850) is now regularly harvested from the bay. Manila clams were introduced to the eastern Pacific as hitchhikers on *Crassostrea gigas* in 1936 (Carlton 1992); they are now cultivated on mid-intertidal flats. As with *C. gigas*, the distribution of Manila clams in Willapa Bay reflects both natural recruitment and planting. Little is known of the historic densities and distributions of other clams, although some insight comes from short periods of harvest records for introduced softshell clams *Mya arenaria* (Linnaeus, 1758) and for native razor clams *Siliqua patula* (Dixon, 1789) and littlenecks *Protothaca staminea* (Conrad, 1837). The 3 major harvested bivalve species allow a comparison, through historical records of yields, of the contributions to secondary production by native and introduced species.

Introduced oysters have been the vector of 2 plant species that occupy what were previously unvegetated mudflats (Fig. 1). The baseline condition for aquatic tracheophytes included native eelgrass *Zostera marina* (Linnaeus, 1753) in pools and extensive beds, generally at and just below mean lower low water (Borde et al. 2003). At upper tidal elevations, an invasive smooth cordgrass *Spartina alterniflora* (Loisel.) has increased rapidly over the past 2 decades, although its unintentional introduction occurred around 1890, presumably as discarded packing material for transplanted *Crassostrea virginica* (Townsend 1893, 1896, Feist & Simenstad 2000). No native *Spartina* species occur in Willapa Bay, and *S. alterniflora* is considered a noxious weed in Washington State, with nearly \$2 million spent annually towards *Spartina* control. A small eelgrass species (*Zostera japonica* [Aschers. et Graebn.]) arrived on the British Columbia coast with transplanted *C. gigas* by 1957, but may have been in coastal Washington even earlier (Harrison & Bigley 1982). In Willapa Bay, it now fills much of the tideflat between *Z. marina* and *S. alterniflora*. Ironically, *Z. japonica* in Washington state enjoys the same protection afforded the native species of eelgrass (Wonham 2003). These 3 plant species allow a comparison, through data on distribution and

growth, of the contributions to primary production by native and introduced species.

We focus on 3 topics relating invasion and ecosystem functioning: (1) primary production by aquatic tracheophytes in Willapa Bay (1 native, 2 introduced species); (2) secondary production by bivalves in the bay (1 native, 2 introduced species); and (3) associated changes in biogenic habitat, detrital production, and filtration capacity. By compiling information from a variety of sources, we are able to estimate primary and secondary production by conspicuous species and how these have changed with the local rise in species richness accompanying introductions.

MATERIALS AND METHODS

Change in primary production in Willapa Bay. The area covered by the 2 eelgrass species was estimated from an unsupervised classification of a LANDSAT satellite image, acquired at low tide (-0.307 m relative to mean lower low water [MLLW]) at 18:30 h GMT (Greenwich mean time) on 5 May 1997 (B. E. Feist & C. A. Simenstad unpubl. data) (Fig. 2). Although it was possible to distinguish eelgrass beds of different density (dense vs. sparse) based on spectral differences, we did not use this information in our calculation of estuary-wide production, because our unit-production estimates came from a range of sites and eelgrass densities in the bay. Because it was not possible to distinguish the 2 species of *Zostera* in the LANDSAT image, we used additional groundtruthing data to determine coverage by each species. An independent assessment of habitat types was carried out by NOAA Coastal Services Center (NOAA CSC 2000) in 1997, which included 20 points within the area we classified as eelgrass and 74 outside. Commission errors were low: only 8 of 53 points without eelgrass were classified as eelgrass present. However, the LANDSAT image classification did miss considerable eelgrass, and only 12 of 41 points with eelgrass were classified as such. Overall, 60% of the points were classified correctly, with some bias towards underestimating total area of eelgrass (no correction to total area was attempted). We determined the percentage of georeferenced points observed to contain each species (55.5% *Z. marina*, 44.4% *Z. japonica*) and multiplied the total area of eelgrass by the fraction represented by each species. For comparison, bathymetric considerations provide an estimate of 4845 ha potentially occupied by *Z. marina* in the 1950s, and 3139 ha, in the 1850s, when bay depths were lower on average (Borde et al. 2003). Our estimate of area covered by *Z. marina* fell within this range (3424 ha), likely at the lower end because other habitat types occupy some of the potential eelgrass zone (0 to -1.2 m MLLW).

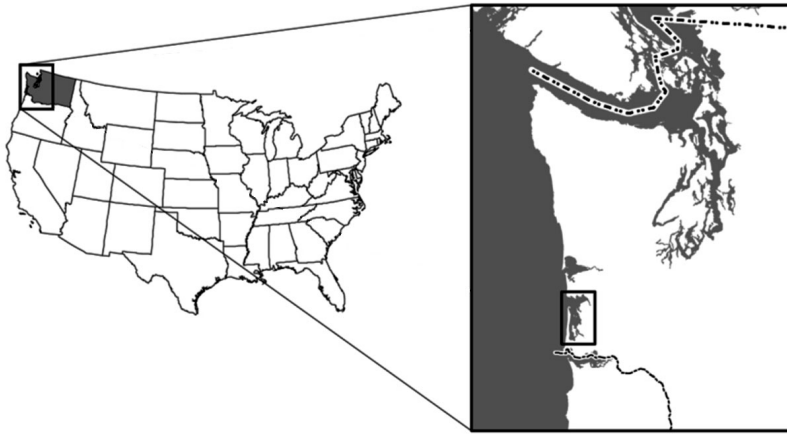
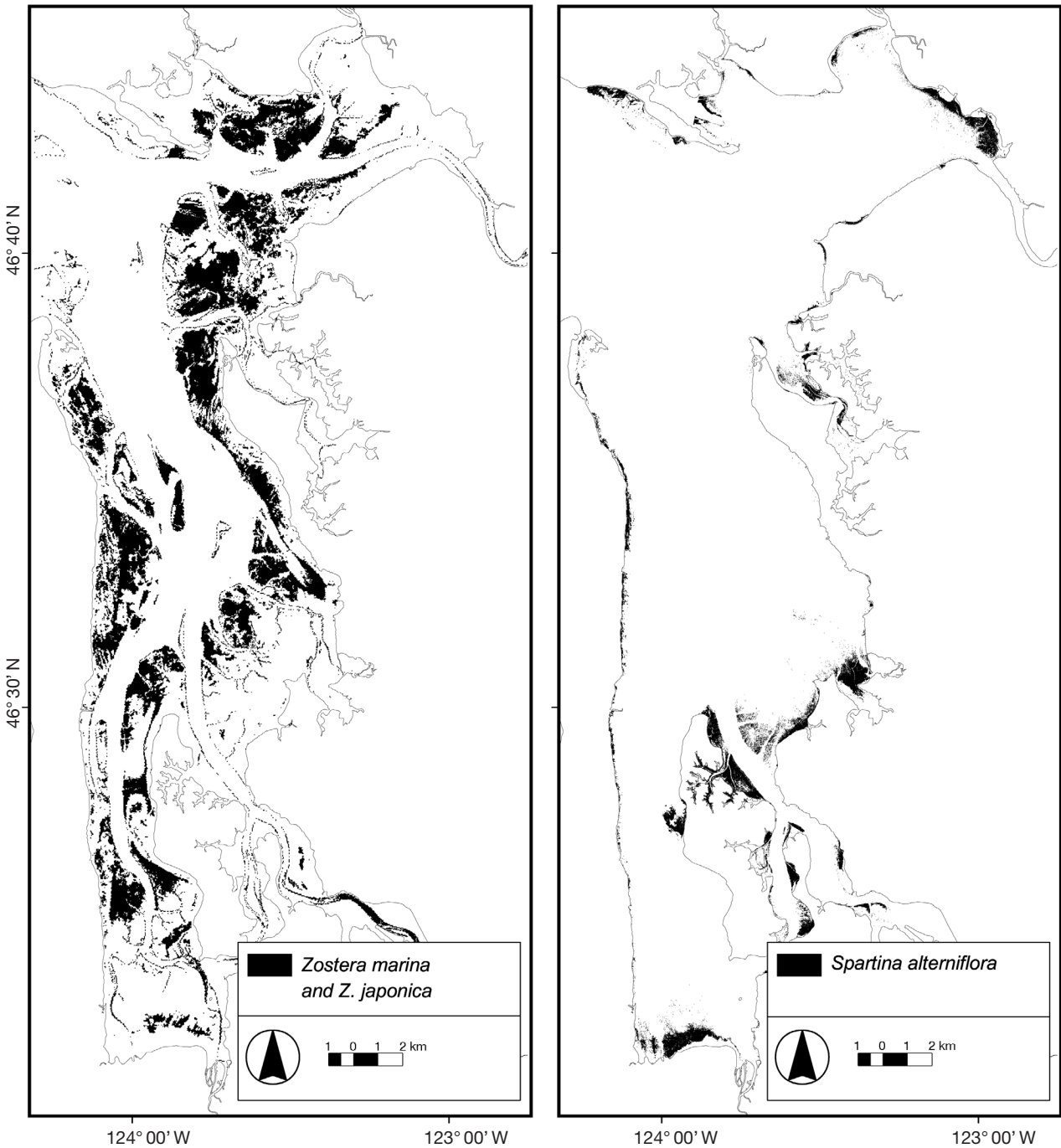


Fig. 2. *Zostera marina* and *Z. japonica* (left panel) and *Spartina alterniflora* (right panel). Distribution of dominant macrophyte species of Willapa Bay, ca. 1997. Inset shows location of Willapa Bay on the west coast of the United States



Annual production of *Zostera marina* on a unit-area basis was derived from shoot densities and growth measured seasonally at 7 locations spread across a distance of 20 km in Willapa Bay. Shoot density was based on the average shoot count in ten 0.25 m² quadrats placed near 0 MLLW at each location. Adjacent to each quadrat, 5 shoots were pricked with an 18 gauge needle at the leaf sheath (Zieman & Wetzel 1980). After 2 to 4 d, these shoots were collected, and growing leaves were separated into original (from needle mark to leaf tip) and new (from leaf sheath to needle mark) material and dried to constant weight at 60°C. The masses of new material were averaged to estimate growth at each site. We measured shoot density and growth 4 times in 2004: winter (February), spring (early May), summer (late June), and autumn (early September). The product of shoot density and growth yielded unit-area production per day in each season. Annual unit-area production was calculated by extending daily measurements to each season, and summing across seasons. Obviously, these calculations require addition and multiplication that complicate calculations of error structure. To avoid problems associated with adding and multiplying error terms, we took a Monte Carlo approach. The entire calculation was repeated 100 times, each time selecting density and growth values at random from among the 7 locations for each season. From these 100 iterations, we calculated a mean and standard deviation. Finally we multiplied this unit-area annual production by the estimated area covered by *Z. marina*.

To assess annual production of *Zostera japonica*, we measured shoot densities and growth at 6 locations across 10 km in Willapa Bay: 3 locations were in the upper range occupied by *Z. japonica*, +1.2 m MLLW, and 3 were at the lower end, +0.6 m MLLW. Because *Z. japonica* blades are too narrow (<1 mm) for the hole-punching technique, we instead used a comparable protocol (Kaldy 2006). Shoots were counted in nine 10 cm diameter areas at each sampling location. Growth was measured in 5 nearby 10 cm diameter areas, distinguished by PVC sleeves pushed 10 cm into the sediment and flush with the surface. We initially trimmed all shoots just above the leaf sheath. After 2 wk, shoots were again counted and trimmed, and the above-ground material was dried to constant weight at 60°C. Growth rate was determined from the amount of new biomass relative to shoot number when the shoots were collected, divided by the number of days between initial and final trims. Because photosynthetic tissue was lost during the initial trim, regrowth may have slowed and growth rates are conservative (Ferraro & Oesterheld 2002). Density and growth were sampled 5 times in 2004: March, May, July, September, and December. These measurements were extrapolated to 2 mo periods (except 4 mo in winter). To estimate above-

ground unit-area primary production, we selected values for density and growth at random from among the 6 locations at each time period. We multiplied density, growth, and the number of days in each season, then summed across seasons. This procedure was repeated 100 times to incorporate uncertainty. We calculated mean annual unit-area production (and standard deviation) from these 100 randomizations, then multiplied by the estimated tidelflat area occupied by *Z. japonica* to generate a production estimate for the entire bay.

The Washington State Department of Natural Resources calculated the total solid area covered by *Spartina alterniflora* in Willapa Bay in 1997 using false-color infrared aerial photographs and ESRI ArcView shapefiles (WADNR 1999) (Fig. 2). This method slightly underestimated coverage because patches of <1.36 m² could not be detected. In contrast to eelgrass, cordgrass loses little of its production during the growing season, instead accumulating tissue above ground before dying back at the end of the year. Consequently, above-ground biomass per area served as a proxy for annual production; these values were available for Willapa Bay in Grevstad et al. (2003), as mean values for 3 locations. We multiplied this production per unit area by area covered by *S. alterniflora* to derive production for the whole bay.

Concerning other tracheophytes, no data are available for primary production in Willapa Bay's tidal marsh, which currently occupies 2484 ha between mean high water and extreme high water (Borde et al. 2003). Marsh plants have been replaced by terrestrial species in areas diked for grazing, but the more recent expansion of introduced aquatic tracheophytes has probably not further altered the contribution of high marsh to primary production in the bay—both introduced species grow below mean high water, whereas in Willapa Bay native marsh occurs above this level (Borde et al. 2003, Zhang et al. 2004, authors' pers. obs.).

Change in secondary production in Willapa Bay.

We estimated annual production of the focal native bivalve (*Ostreola conchaphila*) and introduced bivalves (*Crassostrea gigas* and *Ruditapes philippinarum*) from aquaculture yields in Willapa Bay, as reported to the Washington Department of Fish and Wildlife (Fig. 3). Long-term average yields usually represent a minimum estimate of annual production, because the new biomass in each year must replace the biomass of bivalves removed by harvest. For each species, uncertainty in production was based on interannual variation over a period of 13 to 33 yr (arbitrarily selected as representative of sustained harvest levels), even though this variation may be due more to economic than to ecological conditions. Oyster yields were reported as pounds of shucked meat, which we converted to dry tissue mass by assuming a dry mass:fresh mass ratio of 0.22 (Kobayashi et al. 1997). Clam yields were reported as

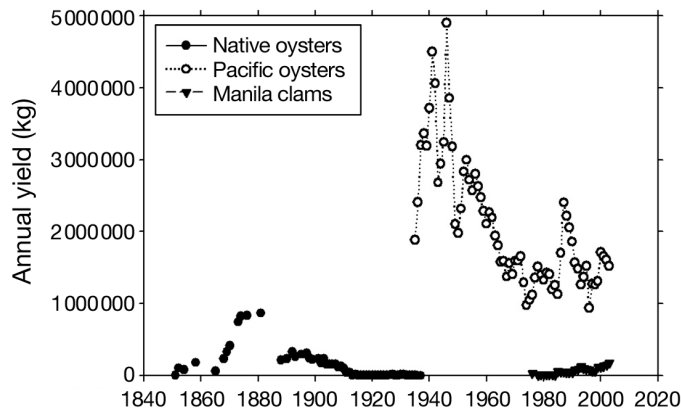


Fig. 3. *Ostreola conchaphila*, *Crassostrea gigas*, and *Ruditapes philippinarum*. Yields of bivalve species from Willapa Bay over 150 yr from Washington Department of Fish and Wildlife marine fish and shellfish landings annual reports. *O. conchaphila* (native oysters) and *C. gigas* (Pacific oysters) are displayed in units of shucked-meat weight (fresh), and *R. philippinarum* (Manila clams) in units of whole-clam weight

pounds in the shell, which we converted to dry tissue mass by assuming a dry mass:whole fresh mass ratio of 0.066 for 40 to 50 mm clams (Solidoro et al. 2003).

Historical trends of other bivalves are mostly unknown because poor records exist even for those species that are occasionally harvested. However, these harvest records for 1980 to 1991 suggest that other bivalves occurred at fairly low densities relative to oysters and Manila clams. For instance, native little-necks *Protothaca staminea* and razor clams *Siliqua patula* averaged 1×10^4 kg live weight harvested per year, ~10% of recent harvests of Manila clams (Fig. 3). Introduced softshell clams *Mya arenaria* were considered for a fishery in the late 1800s, but populations declined abruptly before commercial exploitation began (Palacios et al. 2000).

Other ecosystem functions. Primary and secondary production in estuaries directly influence other ecosystem functions, such as habitat provision, inputs to detrital food webs, and water filtration. To assess changes in habitat, we focused on area occupied by native and introduced species. These data were readily available from LANDSAT and aerial photographs for tracheophytes (see 'Materials and methods Change in primary production in Willapa Bay'), but bivalves have not been similarly mapped. Both native and Pacific oysters recruit naturally in the southern part of Willapa Bay, due to warmer water temperatures and higher larval retention, but aquaculture primarily occurs closer to the mouth of the estuary, where growth rates are rapid (Ruesink et al. 2003).

All primary production was assumed to enter the detrital food web following senescence, because few herbivores consume eelgrass or cordgrass. In addition

to changing detrital biomass, introduced species potentially influence both the timing and the quality (carbon:nitrogen ratio) of dead plant material. This matter may be a source of food or nutrients for some biota, and a source of disturbance to other biota sensitive to wrack burial. We have not quantified detritus fate, but offer a qualitative summary of information on eelgrass- and cordgrass-derived detritus.

Filtration of Willapa Bay's water derives in part from cultured bivalves, and, consequently, we estimated filtration capacity based on secondary production. Filtration rates for each species were not measured directly in Willapa Bay, but a consistent relationship exists between size and filtration rate across many bivalve species (Powell et al. 1992). Consequently, we incorporated individual filtration rates of 3 l h^{-1} for *Crassostrea gigas* (100 mm, 2.4 g dry wt; Kobayashi et al. 1997) and 1 l h^{-1} for *Ruditapes philippinarum* (50 mm, 3.9 g dry wt; Solidoro et al. 2003) and for *Ostreola conchaphila* (50 mm, 0.4 g dry wt; Brennan 1939). We determined the number of individuals of each bivalve species as the ratio of total harvest:individual biomass, and multiplied this estimate of density by per capita filtration rate. We then compared filtration by each species to the bay's total volume ($7.6 \times 10^{11} \text{ l}$ at mean sea level; Hickey & Banas 2003).

RESULTS

Change in primary production in Willapa Bay

The essential components for estimating primary production by aquatic tracheophytes in Willapa Bay included estimates of area occupied and annual production per area. Based on habitat classification from recent satellite images, each eelgrass species occupied about 3000 ha in Willapa Bay, and *Spartina alterniflora* occupied about 1300 ha in 1997 (Fig. 2). Annual rates of production per area were similar for *S. alterniflora*, based on peak standing biomass, and for *Zostera marina* based on seasonal measurements of growth rate ($\sim 1000 \text{ g dry wt m}^{-2} \text{ yr}^{-1}$; Table 1). These rates fall close to other published reports of net primary productivity for *S. alterniflora* (Dai & Wiegert 1996) and *Z. marina* (Kentula & McIntire 1986, Thom 1990). Production for *Z. japonica*, which reaches a high density but is a very small plant, was much lower ($\sim 170 \text{ g dry wt m}^{-2} \text{ yr}^{-1}$), but was also similar to previous production estimates (Thom 1990).

We estimated that native eelgrass *Zostera marina* produced >35 000 t of dry matter annually in Willapa Bay (Table 2). The 2 introduced species appear to have recently raised primary production by aquatic tracheophytes by >50%. The cordgrass *Spartina alterniflora*

Table 1. Components of production by dominant macrophytes in Willapa Bay. Mean and standard deviation (SD) for shoot density and growth were calculated from N sites (in square brackets) throughout the bay. SD (in parentheses) for annual production per area of eelgrass was based on 100 Monte Carlo randomizations of values for each variable contributing to the calculation of annual production, specifically shoot growth and shoot density in different seasons

Species	Area (ha)	Period	Production per area	
			Shoot density (m ⁻²)	Shoot growth (mg dry wt shoot ⁻¹ d ⁻¹)
<i>Zostera marina</i>	3423.6	Winter	161.7 (30.4) [6]	3.03 (0.545) [5]
		Spring	141.9 (30.2) [7]	24.3 (9.18) [7]
		Summer	159.5 (33.9) [7]	35.8 (15.0) [7]
		Autumn	105.4 (35.9) [7]	14.9 (4.19) [7]
		Annual	Biomass, g dry wt m ⁻² : 1.03 × 10 ³ (0.40 × 10 ³)	
<i>Zostera japonica</i>	2738.8	Mar	2242 (1211) [6]	0.0955 (0.0200) [6]
		May	3271 (1718) [6]	0.2026 (0.0529) [6]
		Jul	5996 (1870) [6]	0.2127 (0.0667) [6]
		Sep	3624 (2132) [6]	0.1594 (0.0607) [6]
		Dec	1931 (653) [6]	0.0487 (0.0178) [6]
Annual	Biomass, g dry wt m ⁻² : 1.75 × 10 ² (0.51 × 10 ²)			
<i>Spartina alterniflora</i>	1298.5	Annual	Biomass, g dry wt m ⁻² : 1.01 × 10 ³ (0.49 × 10 ³) [3]	

was estimated to produce an annual standing crop in excess of 13 000 t, and the small-sized introduced eelgrass *Z. japonica* was estimated to produce nearly 4800 t, increases of 37 and 14 %, respectively. Considerable uncertainty exists around these average values, particularly due to spatial variation in shoot density (Table 1). However, the additional production estimated from introduced species exceeds the variation (standard deviation) within species.

Change in secondary production in Willapa Bay

Recent yields of Pacific oysters and Manila clams from Willapa Bay far outweigh historical landings of native oysters (Fig. 3, Table 2). The annual yield of introduced *Crassostrea gigas* at the end of the 20th century was almost 4 times higher than annual yields of

native *Ostreola conchaphila* at the end of the 19th century. *Venerupis philippinarum* actually contributed little additional production, even though landings since 1985 have increased about 6 % annually. We estimated that native oysters used to produce about 92 t of dry matter annually, excluding shells. Secondary production from native oysters has largely disappeared, but introduced bivalves, particularly *C. gigas*, currently generate 330 t yr⁻¹. Clearly, this secondary production is dwarfed by the primary production of aquatic tracheophytes, which have production values >2 orders of magnitude higher.

Other ecosystem functions

Habitat

Willapa Bay contains extensive intertidal flats, and, in the absence of introduced species, 39% of the bay's area would consist of unstructured intertidal habitat (Borde et al. 2003). In our spatial analyses, native *Zostera marina* occupied 9.6% of the bay's area (>3400 ha of 35 700 ha; Table 1), and tidal flats have been modified by introduced *Z. japonica* (7.7% of bay area) and *Spartina alterniflora* (3.6%). Areas intensively cultivated for bivalves occupy 10% (Feldman et al. 2000), and, because both native and non-native species have been cultivated in these areas, we believe there has been little trend in cultivated area over the past century (Townsend 1896, Hedgpeth & Obrebski 1981). However, wild populations of native *Ostreola conchaphila* were reportedly subtidal, accessible only at extreme low tides (Collins 1892), whereas hummocks of introduced *Crassostrea gigas* occur intertidally (authors' pers. obs.). Thus, oyster habitat has shifted from sub-tidal to intertidal areas where oysters recruit naturally, but precise dimensions are not available.

Table 2. Estimated annual production (prod.) by dominant macrophyte and bivalve species in Willapa Bay. No sample sizes (N) are provided for primary production because SD (in parentheses) was based on Monte Carlo randomizations. For secondary production, N (in brackets) is number of years of sustained harvests

Species	Native/ Introduced	Years of measurements		Annual production (kg dry wt yr ⁻¹)
		Area	Prod.	
<i>Zostera marina</i>	Native	1997	2004	3.53 × 10 ⁷ (1.37 × 10 ⁷)
<i>Zostera japonica</i>	Introduced	1997	2004	4.79 × 10 ⁶ (1.40 × 10 ⁶)
<i>Spartina alterniflora</i>	Introduced	1997	2001	1.31 × 10 ⁷ (0.63 × 10 ⁷)
<i>Ostreola conchaphila</i>	Native	1866–1900		9.16 × 10 ⁴ (0.54 × 10 ⁴) [16]
<i>Crassostrea gigas</i>	Introduced	1971–2003		3.23 × 10 ⁵ (0.72 × 10 ⁵) [33]
<i>Ruditapes philippinarum</i>	Introduced	1991–2003		6.94 × 10 ³ (0.22 × 10 ³) [13]

These new habitats influence the entire community composition of smaller estuarine organisms. For instance, epibenthic organisms are more diverse on *C. gigas* than in open mudflats (Hosack 2003). Estuarine invertebrates respond to *S. alterniflora* and *Z. japonica* in complicated ways: some species increase and some decline relative to nearby mudflats, but, as with oysters, the overall effect is to alter community structure (Posey 1988, Wonham 2003).

Detritus

The calculated increase in the bay's macrophyte production over the past century due to invaders likely had a concomitant effect on detritus. In addition to the overall increase in detrital biomass (>50%), both the type and timing of detrital production have changed. *Zostera japonica* detritus has a lower C:N ratio (C. J. Harvey unpubl. data) and more rapid decomposition than the native eelgrass (Hahn 2003). In contrast, *Spartina alterniflora* has a higher C:N ratio than *Z. marina* (C. J. Harvey unpubl. data). Rather than producing detritus throughout the growing season, *S. alterniflora* accumulates biomass, and detritus appears in autumn. In Willapa Bay, wrack builds up substantially on beaches, where its effects on plant regeneration and invertebrate communities are presumably similar to those in its native range (Ranwell 1967, McCaffrey 1976). Wrack-burial disturbance has been shown to alter salt marsh structure (Boston 1983), plant zonation and community structure (Brewer et al. 1998, Pennings & Richards 1998), sediment chemistry (Pennings & Richards 1998), and plant clonal morphology (Brewer & Bertness 1996). Prior to the arrival of *S. alterniflora*, Willapa Bay was not subjected to heavy annual inputs from wrack generated by marsh plant dieback.

Filtration

The filtration capacity of bivalves can substantially influence the overall state of an estuary (Jackson et al. 2001). Scaling up to annual yields, we estimated that native oysters could have filtered 6.0×10^9 l d⁻¹ prior to exploitation, and the 2 introduced bivalves filter at least 9.7×10^9 l d⁻¹. Daily, these respective rates would affect 0.8 and 1.3% of the bay's volume (7.6×10^{11} l at mean sea level; Hickey & Banas 2003). Although these percentages appear small, they only account for feeding by harvested bivalves, leaving out unreported collections, beds where bivalves have not reached market size, feral populations, and other suspension-feeding species. The calculated difference in historic and cur-

rent filtration rates is less than the difference in yield, because smaller individuals (e.g. native oysters) have higher per biomass filtration than larger individuals (e.g. Pacific oysters).

DISCUSSION

Primary and secondary production in heavily invaded estuaries

As new species entered Willapa Bay over the past century, total primary production by focal aquatic tracheophytes increased by >50%, and total secondary production by focal bivalves increased by 250%, despite the decline of the native oyster (Table 2). In fact, we have likely underestimated change in secondary production: harvested biomass was not sustainable for native oysters, suggesting it overestimates historical production, whereas introduced oysters and clams occur in feral populations outside aquaculture, and harvested biomass likely underestimates current production. Of course, these calculations for macrophytes and bivalves include just 1 native and 2 introduced species in each case, and they do not account for diverse additional native and non-native species. However, it is extremely unusual to know whole-ecosystem production for even 6 species, and the contributions from other bivalves and tracheophytes appear to be small and/or relatively stable over the past 50 yr (see 'Materials and methods').

More generally, none of the introduced species we examined fully occupies its potential habitat in Willapa Bay, so there may be capacity for further increases in production. Such is particularly true of tracheophytes, which continue to expand rapidly. In 2000 relative to 1997, the area of *Spartina alterniflora* in Willapa Bay increased by 23% (to 1601 ha; WADNR 2003). Given a total intertidal area of 18 200 ha, perhaps half of which is potentially invasible by cordgrass, annual production could increase by up to 6-fold if left uncontrolled. According to analyses by Pacific County (in Hedgpeth & Obrebski 1981), oyster yields (and therefore secondary production) could be enhanced by an order of magnitude, although oyster expansion is constrained by the availability of settlement substrate, and will lag behind expansion of tracheophytes unless there are changes in aquaculture practices. Furthermore, recent oceanographic models of the bay indicate that increased biomass could come at the expense of slowed individual growth rates (N. S. Banas et al. unpubl. data).

The introduced species considered here have modified production, and likely a variety of other ecosystem processes, because they consist disproportionately of ecosystem engineers (Jones et al. 1994, Gutierrez et al.

2003, Cuddington & Hastings 2004). Both macrophytes and oysters provide biogenic structure and modify their local environment in self-reinforcing ways, for instance by accumulating sediment (*Spartina alterniflora*; Zipperer 1996) or providing hard substrate for recruitment (oysters; Mobius 1883). The introduced species of bivalves and tracheophytes in Willapa Bay may play particularly high-impact roles, because these tideflats were previously unstructured (Fig. 1), and the new species do not simply replace native species, which tend to be restricted to different tidal elevations. The previously unstructured mudflats certainly supported other primary producers and filter feeders in the past. Given our reliance on harvest records and remote-sensing data to estimate production for even the most prolific introduced species, we cannot make quantitative estimates of production changes for benthic diatoms, small native bivalves, burrowing shrimp, or other filter- or deposit-feeding infauna. Nor can we conclude how the production rates of organisms associated with new substrates (e.g. benthic diatoms, macroalgae, and filter feeders living on oyster shell substrates; epiphytes living on *Zostera japonica*) compare with rates on open mudflats without further study.

Ecological theory suggests that environments with free resources (empty niches) are particularly susceptible to invasion (Shea & Chesson 2002), and new species that modify their environment to their own benefit have particularly high impacts (Crooks 2002, Cuddington & Hastings 2004). Our data directly indicate how species that play novel roles in an ecosystem can affect production, with further implications for habitat, detritus, and filtration. For example, *Crassostrea gigas* reefs and culture sites provide extensive, otherwise unavailable hard substrate for fish, invertebrates, and macroalgal species such as *Ulva* spp. and *Enteromorpha* spp., both of which have become abundant in intertidal zones where *C. gigas* culture or hummocks are present. In addition, Willapa's introduced engineers probably also affect biogeochemical cycles. In another coastal estuary, introduced *Zostera japonica* serves as a sink for water-column nutrients (Larned 2003), and bivalves can store nutrients in biodeposits (Chapelle et al. 2000), or, at high densities, enhance nutrient release (Bartoli et al. 2001). Furthermore, oyster expansion has occurred at the expense of burrowing shrimp and other infauna, undoubtedly causing changes in sediment porosity and bioturbation and further affecting biogeochemistry (Webb & Eyre 2004).

The Willapa Bay case history is also compelling, because similar shifts in ecosystem function are likely occurring in other tideflat-dominated estuaries where these and other introduced species have become established (e.g. Cohen & Carlton 1995, Castillo 2000). We expect that this same suite of introduced species

will have, or is already having, similar effects in other estuaries in the region, many of which have comparable native taxa, aquacultural practices, geological ages, tidal amplitudes, and sediment-accretion rates (e.g. Emmett et al. 2000), and often much greater levels of human activity and anthropogenic disturbance. It is possible to imagine additional engineering species that could further transform west coast tideflats, such as burrowing fiddler crabs (e.g. McCraith et al. 2003).

Biodiversity–ecosystem function relationships for native and non-native species

Most conceptual models and much empirical data about the relationship between biodiversity and ecosystem functioning portray a linear or asymptotic curve (Hooper et al. 2005). In native systems, we expect ecosystem processes to asymptote as species richness increases, due to competition for and partitioning of space and other resources among functional group members. In contrast, in invasion biology, it is well recognized that a small proportion of introduced species have disproportionately high impacts (Williamson & Fitter 1996). Thus, the expansion of primary producers and filter feeders higher into the intertidal zone of Willapa Bay represents a step change in several major ecosystem processes. A small number of highly successful invaders has dramatically altered ecosystem processes even though species richness increased only slightly (Fig. 4). Such step functions are by-products of the invaders' typically high rates of productivity, fecundity, and dispersal relative to the native community (Mack et al. 2000), particularly if they play a novel ecosystem role. Additionally, inherent differences between closely related native and introduced species can magnify the impact of the introduction; in the present case, the total area occupied by *Crassostrea gigas* under cultivation (~10% of bay area; Feldman et al. 2000) probably does not greatly exceed the historical area of native oysters. However, there are profound

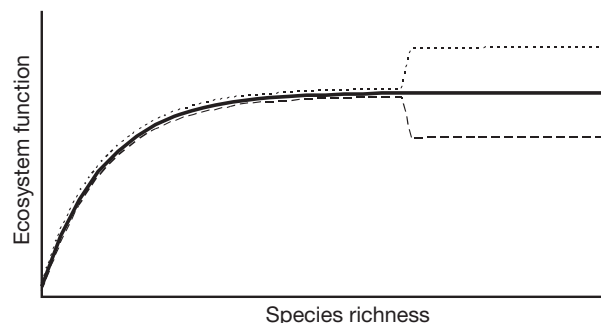


Fig. 4. Step change in ecosystem functioning associated with the introduction of a high-impact species to an otherwise intact ecosystem

biological differences between the 2 oyster species that drastically affect their ecological impacts: *C. gigas* grows several times faster (Ruesink et al. 2005, A. C. Trimble et al. unpubl. data), reaches a larger maximum size (30 vs. 6 cm; Baker 1995), and has greater desiccation and temperature tolerance (Korringa 1976) than *Ostreola conchaphila*. These 2 branches of thought in community ecology—one emphasizing the role of species or functional group richness and the other emphasizing the high impacts of particular species—remain unreconciled.

Three considerations may help reconcile research focused on biodiversity versus invasion: scale, trophic complexity, and real differences in how native and non-native species affect ecosystem processes. The 'scale' issue reflects methodological differences: biodiversity–ecosystem function studies have been carried out by comparing species richness across sites or experimentally manipulating the number of species locally (Stachowicz et al. 2002, Duffy et al. 2003, Raffaelli et al. 2003), generally by random removal of species (but see Solan et al. 2004). Invasion biology tends to emphasize impacts at the level of a site, and there is by necessity biased selection of study species that have high impacts. Thus, invasion biologists find that particular species matter because that is the hypothesis they test. Trophic complexity is generally low in biodiversity–ecosystem function studies, where suites of species compete for a common resource. In contrast, many high-impact invaders are consumers and thus introduce new trophic roles into a community. It should be noted, however, that studies of multiple trophic levels of native species have also shown that consumer impacts can trump species richness in determining production (Paine 2002). So, different amounts of trophic complexity incorporated in study design may also explain differing results. Finally, it is possible that native species with a long history of coevolution do indeed interact differently than non-natives entering a novel recipient community. This leads to the expectation that, while both native and non-native species can influence ecosystem processes, native species do so primarily through resource use efficiency and non-natives through sampling effects. Resource use efficiency would be expected in a group of species that has had the opportunity to adapt, specialize, and partition resources (Ruesink & Srivastava 2001). In contrast, in newly introduced species, production might improve primarily through a sampling effect, because a small proportion of exotics strongly influences ecosystem functioning. A major research need is for small-scale studies that explicitly address patterns of production across richness levels of native species versus natives and non-natives combined.

Because the Willapa Bay community has been irreversibly altered, it is difficult to reconstruct the biodiversity–ecosystem function relationship for native species alone. However, the tremendous amount of habitat available to invasion makes it very likely that step functions have occurred in functions such as primary production, detritus generation, filtration, and sediment–water exchanges (Fig. 4). These step functions derive from gains in species, rather than from losses. Some previously important species have declined in abundance, but none has been eliminated entirely. Evidence from other systems suggests more attention should be paid to ecosystem responses as species invade. Outside of islands and lakes, introduced species rarely cause outright extinction, although they often change the relative abundance of species and therefore diversity (Wilcove et al. 1998, Gurevitch & Padilla 2004). Consequently, local invasions exceed extinctions for many taxa (Sax et al. 2002), and theory also suggests that global biotic homogenization will tend to enhance local richness (Rosenzweig 2000).

Management response

Changes in production in Willapa Bay have had substantial economic consequences, as well as ecological. In general, management is directed at fostering the production of bivalves and reducing the production of tracheophytes (even though these species all provide valuable ecosystem functions where they are native). Introduced *Spartina alterniflora* is targeted for control with herbicides, estimated at about 4000 l of imazapyr in 2004 (Hedge et al. 2003, Patten 2003). In contrast, introduced bivalves are planted for economic benefit, which on a local scale precludes production by other species. Dredging during oyster culture can remove native eelgrass, which is protected under a Washington state policy of no net loss (Pawlak & Olson 1995), and pesticides (2000 kg of carbaryl annually around 1990; WDF/WDOE 1992) are sprayed to kill native burrowing shrimp *Neotrypaea californiensis* (Dana, 1854), a 'pest' species that displaces eelgrass and smothers oysters (Feldman et al. 2000, Dumbauld & Wyllie-Echeverria 2003).

Within taxa, management also differs. At the same time that millions of dollars are being spent on *Spartina* control, *Zostera japonica*, another introduced macrophyte in a similar habitat, is protected in Washington (Wonham 2003). Our analysis suggests that the discrepancy stems in part from *S. alterniflora*'s higher production and therefore impact in Willapa Bay (Table 2). Similarly, introduced species of oysters and clams are being farmed in preference to native species. Here too, relative productivity may weigh heavily in aquaculturists' decisions (Table 2).

The lesson from *Spartina alterniflora* and *Zostera japonica* is that alterations of the food web can cause management problems, which are difficult to reverse. New species should be introduced with caution, and spread of established invasive plants should be controlled. The lesson from *Crassostrea gigas* and *Ruditapes philippinarum* is that careful planting (preventing overexploitation) and protection of water quality can result in sustained estuarine resources for humans. While these bivalves cannot be eliminated, due to their economic importance and widespread distribution, it is possible that many feral oysters could be removed and native oysters could be restored in subtidal areas. Humans depend on the productivity of the earth's living systems, including estuarine ecosystems, and they also transform the local species involved in production, both intentionally and unintentionally, through introductions. The challenge facing managers is to determine cumulative risk, where the impacts of introduced species on native species, estuarine biodiversity, and ecosystem function are viewed in the context of all the perturbations, natural and anthropogenic, that affect estuaries.

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