Elkhorn Slough
150 km South
of S.F. 395
(estuary)

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Biological invasions of estuaries without international shipping: the importance of intraregional transport

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Abstract

Increased awareness of the problem of introduced marine species has led to recent surveys of several large bays with international shipping. To our knowledge, no thorough search for introductions has been carried out in an embayment *not* connected to an international harbor. In 1998, we investigated the macroinvertebrate fauna of Elkhorn Slough (ES), an estuary in central California. Fieldwork and a literature review revealed 56 known exotic species at ES, a surprising diversity considering the rather modest search effort, the relatively natural setting of this estuary, and the lack of international shipping. While some exotic species at ES were probably introduced directly from distant waters with cultivated oysters, others likely arrived more indirectly via San Francisco Bay or other regional ports with thriving populations of invaders, travelling for instance as adults fouling boats or as larvae on currents. The effect of international shipping, including ballast water dumping, is thus not limited to areas with major harbors, but rather reverberates up and down the coast to seemingly isolated embayments.

Keywords: Biological invasions; Exotic species; Elkhorn Slough; Ballast water; Invertebrates

1. Introduction

Exotic marine organisms are ubiquitous in bays with large harbors supporting intensive international shipping. For example, about 150 nonindigenous invertebrates have been documented in San Francisco Bay, California (Cohen and Carlton, 1995), 100 in Pearl Harbor, Hawaii (Coles et al., 1997), 50 in Puget Sound, Washington (Cohen et al., 1998), and 100 in Port Phillip Bay, Australia (Hewitt et al., 1999). These invaders arrived by various means, including aquaculture and ship-hull fouling. Recently, however, the most significant mechanism of introduction has been ballast water (Carlton, 1985; Ruiz et al., 1997), which is pumped and gravitated into vessels at one port, and discharged at another, transporting planktonic and nektonic organisms (as well as benthic organisms in sediments inadvertently taken in with the water) between regions. As a result of these human-mediated introductions, the fauna of many harbor areas has become homogenized as native species are reduced in abundance and habitat breadth (Ruiz et al., 1997).

The problem of invasions in major harbors and associated bays is gaining increasing recognition, but the degree to which the problem also exists in small bays with little or no international shipping is not well known. Are invaders also diverse and abundant in the smaller estuaries and bays that lie between major shipping ports? In the northeastern Pacific region, some exotic species have been identified and studied in smaller embayments (e.g. Carlton, 1979; Grosholz and Ruiz, 1995; Byers, 1999), but few if any systematic broad-scale, multi-taxon searches have been carried out in such places. Since direct transport from distant waters via international ship fouling or ballast water is uncommon at such embayments, the diversity of invaders might be lower. However, exotic species may become established at smaller embayments through other direct mechanisms, such as culturing of oysters

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brought in from other regions. Exotic species may also arrive indirectly via intraregional transport; in particular, invaders introduced to a major port by shipping may spread along the coast once established (Cohen and Carlton, 1995; Grosholz and Ruiz, 1995; Hewitt et al., 1999). Such secondary transport may occur by natural mechanisms such as movement of adults or larvae, or by anthropogenic mechanisms such as exchange of commercial oyster stocks by growers in different bays or travel between harbors by boats carrying organisms on their hulls or in their live-well water.

We investigated the exotic invertebrate fauna at Elkhorn Slough (ES), California, an estuary about 150 km south of San Francisco Bay (SFB). ES has had a long history of oyster culture, now abandoned, and there is a small harbor for fishing and recreational boats at its mouth. We compared the exotic fauna of ES to that of SFB (1) to determine whether the absence of international shipping and particularly ballast water dumping has protected ES from being as severely invaded as SFB, and (2) to explore whether the proximity of SFB with its well-established populations of exotic species has affected the species composition of ES.

2. Methods

2.1. Characterization of Elkhorn Slough

Elkhorn Slough (ES) is a large coastal wetland located in central California, just inland of Moss Landing Harbor at the midpoint of the Monterey Bay (Fig. 1). Its history, biology, and physical setting have been well characterized (Schwartz et al., 1986, Silberstein and Campbell, 1989, Caffrey et al., 2001). Drainage from the old Salinas River channel (site 1, Fig. 1) supplies freshwater year-round near Moss Landing (site 2) at the mouth of the slough. The upper reaches of ES (e.g. site 10) are sometimes hyposaline in the rainy season and sometimes hypersaline in the dry season. However, freshwater input to ES is minor compared to the tidal prism, and the majority of ES wetland habitats are essentially marine due to strong tidal flushing, especially along main channel (e.g. sites 4, 8, 9). Water quality is influenced by runoff from adjacent farmlands; extremely high nutrient, pesticide, and coliform bacterial levels have been documented. About 500 native species of marine invertebrates have been reported from ES (Caffrey et al., 2001).

2.2. Collection, identification, and categorization of invertebrates

We searched intensively for invertebrates at ten intertidal sites at ES (Fig. 1) during two consecutive low spring tides in March, April, May and July 1998. We estimate that about 10 person-hours were spent searching during each of these four sampling periods. In the subsequent 2 years, we occasionally searched for invertebrates; we estimate that about 10 additional hours were spent searching in these later miscellaneous efforts. Therefore, the total field search effort for this study sums to 50 person-hours.

At each site, we looked for any intertidal or shallow subtidal invertebrates we could find, usually focusing on organisms on rocks, pilings, or other available hard substrates, since an extensive previous study (Nybakken et al., 1977) had rigorously investigated the infaunal community of ES. We collected specimens of all species we did not confidently recognize as natives. The specimens were microscopically examined at Long Marine Laboratory in Santa Cruz, and were identified using Light's Manual (Smith and Carlton, 1975) and additional references from the primary literature when necessary. Difficult specimens were sent to taxonomic experts for identification. We deposited voucher specimens of all exotic and cryptogenic species we collected in the California Academy of Sciences (catalogue numbers 144150-144188).

In addition to this fieldwork, we carried out a literature review for exotic species at ES. We looked for the first reference to the presence of each exotic species, which often originated from MacGinitie's (1935) classic work at ES or from Nybakken et al. (1977). From our fieldwork and literature search, we complied a list of exotic invertebrates (Table 1), mostly using the designations

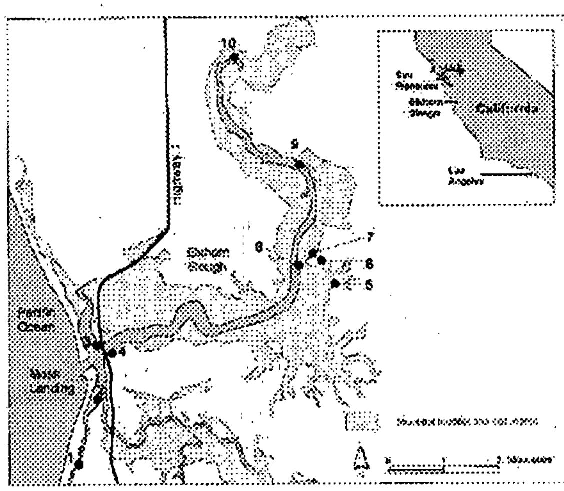

Fig. 1. Location of collection sites at Elkhorn Slough, California. Numbering of sites corresponds to Table 1. The exact location of these sites is as follows: 1, north side of bridge over old Salinas River channel, just south of Moss Landing; 2, Moss Landing Harbor; 3, "Skipper's", just northwest of Highway 1 bridge; 4, "Vierra's", just southeast of Highway 1 bridge; 5, area around footbridge on South Marsh trail; 6, Whistlestop Lagoon, 7, "Batillaria Heaven", mud pan on Hummingbird Island; 8, main channel of Slough at shore of Hummingbird Island; 9, Kirby Park, near boat ramp; 10, Hudson's Landing, just west of Elkhorn Road.

of previous authors (especially Smith and Carlton, 1975; Cohen and Carlton, 1995) to determine whether a species was native to the northeastern Pacific. For species not listed in these references, we made our own determinations as follows: species with very disjunct global distributions, not previously recorded at ES and described originally from distant localities, were considered exotic, while those with somewhat disjunct or cosmopolitan distributions were considered cryptogenic (*sensu* Carlton, 1996: a cryptogenic species is one whose origin cannot readily be determined with available data). We examined patterns of invasion over time for all ES exotic species, and assessed native ranges and likely transport mechanisms for each species based on the literature, relying heavily on determinations made by Cohen and Carlton (1995).

2.3. Comparison to San Francisco Bay (SFB)

We compared our exotic species list for ES to that of Cohen and Carlton (1995) for SFB. For the purposes of this comparison, we omitted 16 SFB species (from their list of 147 invertebrates) that are limited to freshwater habitats, which are absent from ES. We also eliminated from the analysis three species-complexes (the jelly *Aurelia aurita*/*Aurelia* sp.; the hydroid *Obelia* spp.; the clam *Macoma balthica*/*Macoma petalum*) found in both studies. These complexes each consist of native and exotic species that are so morphologically similar that they cannot readily be distinguished without molecular methods.

We compared species richness and species composition of exotic invertebrates between ES and SFB. To determine whether there were differences in origins of invaders, we used a χ^2 contingency analysis to compare native ranges of the total exotic species found in ES vs. SFB. To compare frequency of different transport mechanisms for the two estuaries, we carried out two χ^2 contingency analyses for ES vs. SFB invaders. To determine whether species found only in SFB were associated with different transport mechanisms than those also found in ES, we used another χ^2 contingency analysis to compare transport mechanisms of exotic species found *only* in SFB (not ES) vs. those found in *both* SFB and ES.

3. Results

A total of 56 exotic invertebrate species are now known from Elkhorn Slough (Table 1). In our fieldwork, we collected 34 exotic species and six cryptogenic species. Of these, 19 of the exotic and four of the cryptogenic species had not previously been reported for ES. We found nearly half of these previously unreported species during our first sampling period in March 1998, and the rest spread fairly evenly between April, May, and July 1998 and miscellaneous later efforts (Fig. 2). On average, we collected about one previously unreported species for every 2 h of search effort. Our literature review revealed 16 additional exotic species reported for ES. We also learned of six invaders found by others at ES but never reported in the literature (listed as personal communications in Table 1).

It is difficult to determine when each of these 56 species first became established at ES. Fig. 3 shows the number of new invaders at ES per year reported in published literature. The largest peaks are in 1935, 1977, and 2001, representing MacGinitie's, Nybakken et al.'s, and our studies, respectively. The new species reported by each study were likely present well before publication, so this graph cannot be read as an accurate representation of the specific timing of invasions. However, the general temporal trends are probably reliable; invasions have occurred continuously over this whole period, certainly without a decline, and perhaps even with an increase over time.

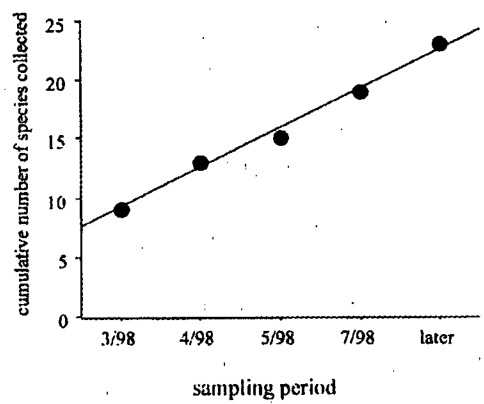

Fig. 2. Cumulative number of previously unreported exotic and cryptogenic species collected at Elkhorn Slough in the current study, by sampling period. About 10 person hours were spent searching in the field during each period. A linear regression model provides an excellent fit to the data ($R^2=0.99$, $P=0.0004$), indicating that the cumulative number of new species collected increased consistently with net search effort.

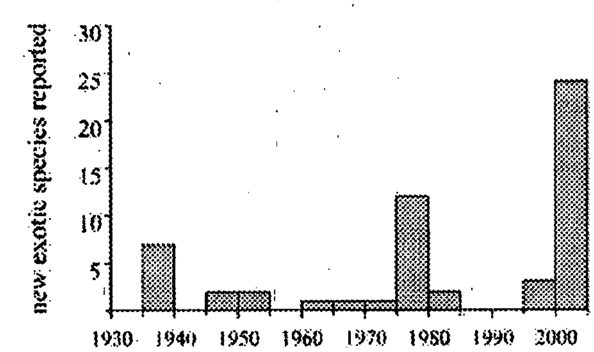

Fig. 3. Number of new exotic species reported in the literature for Elkhorn Slough each year.

Table 1
Exotic and cryptogenic species of Elkhorn Slough[a]

Taxon	Species	Sites	Reference	Transport		
				OC	SF	BW
Exotic invertebrates						
Porifera	*Cliona celata*[b]		Nybakken et at., 1977	X		
	Halichondria bowerbanki	5, 6, 9	MacDonald and Nybakken, 1978; this study	X	X	
	Haliciona ?loosanoffi	4–6, 9	This study	X	X	
	Hymeniacidon ?sinapium[c]	5, 6	This study	X	X	
Cnidaria: Hydrozoa	*Cordylophora caspia*	1	This study		X	X
	Ectopleura crocea	3–5, 9	MacGinitie, 1935; Canton, 1979; this study	X	X	
Anthozoa	*Diadumene franciscana*	5	This study		X	X
	Diadumene leucolena	4, 7	This study	X	X	X
	Diadumene lineata	4, 5, 7, 9	Ricketts and Calvin, 1939; Carlton, 1979, this study	X	X	
Platyhelminthes: Trematoda	*Cercaria batillariae*[c]		J. Byers, personal communication	X		
Annelida: Polychaeta	*Ficopomatus enigmaticus*	1, 9, 10	J. Alicea. personal communication, this study		X	
	Heteromastus filiformis		Nybakken et al., 1977	X		X
	Polydora ligni		Carlton, 1979	X	X	X
	Pseudopolydora paucibranchiata		Blake and Woodwick 1975; Carlton 1979	X	X	X
	Streblospio benedicti	5, 9	Blake and Woodwick, 1975; Carlton, 1979; this study	X	X	X
Mollusca: Gastropoda	*Urosalpinx cinerea*[b]		Burch, 1945b; Smith and Gordon, 1948; Carlton 1979	X		
	Batillaria attramentaria[c]	1 – 10	McLean, 1960; Carlton, 1979; Byers, 1999; this study	X		
	Okenia plana	9	This study	X	X	X
	Philine auriformis	8	This study			X
	Tenellia adspersa	9	Carlton 1979; this study		X	X
	Myosotella myosotis	2	Burch, 1945a; Carlton, 1979; this study	X	X	
Bivalvia	*Gemma gemma*	5, 9, 10	MacDonald, 1969; Carlton, 1979; this study	X		
	Lyrodus pedicellatus		MacGinitie, 1935; Carlton, 1979		X	
	Musculista senhousia[b]		Carlton, 1979	X		
	Mya arenaria[b]		MacGinitie, 1935; Carlton, 1979	X		
	Mytilus galloprovincialis	1–6, 9	Suchanek et al., 1997; this study		X	X
	Venerupis philippinarum	4	Shaw, 1950; Carlton, 1979; this study	X		
Crustacea: Copepoda	*Mytilicola orientalis*		Katkansky and Warner, 1974; Carlton, 1979	X		
Cirripedia	*Balanus improvisus*	4, 5	This study	X	X	
Tanaidacea	*Sinelobus* sp.		P. Slattery, personal communication		X	X
Isopoda	*Iais californica*	5, 6, 9	This study		X	
	Limnoria quadripunctata		MacGinitie, 1935; Carlton, 1979		X	
	Sphaeroma quoyanum	1, 5, 6, 9, 10	This study		X	
Amphipoda	*Ampithoe valida*		P. Slattery, personal communication	X	X	X
	Caprella mutica		Marelli, 1981; Cohen and Carlton, 1995	X		X
	Corophium acherusicum		Nybakken et al., 1977; Carlton, 1979	X	X	
	Corophium insidiosum		Nybakken et al., 1977; Carlton 1979	X	X	
	Corophium uenoi[c]		Nybakken et al., 1977; Carlton, 1979	X		
	Grandidierella japonica	9	This study	X	X	X
	Jassa marmorata		J. T. Carlton, personal communication		X	X
	Melita nitida		Carlton, 1979; Chapman, 1988	X	X	X
	Parapleustes derzhavini		P. Slattery, personal communication		X	
Decapoda	*Carcinus maenas*	5, 6, 9, 10	Grosholz and Ruiz, 1995; this study			X
	Palaemon macrodactylus		Standing, 1981			X
Bryozoa	*Amathia vidovici*[c]	5, 6, 9	This study		X	
	Bowerbankia gracilis	3-6, 9	MacGinitie, 1935; this study	X	X	
	Bugula "neritina"	4-6, 9	This study	X	X	
	Bugula stolonifera	4, 5, 9	This study		X	
	Conopeum tenuissimum	2-6, 9	This study	X	X	X
	Cryptosula pallasiana	5, 6	This study	X	X	
	Schizoporella unicornis	3, 5, 9	Osburn, 1952; this study	X	X	
	Watersipora "subtorquata"	2 – 6	Cohen and Carlton, 1995; this study		X	
Kamptozoa	*Barentsia benedeni*	10	This study	X	X	
Chordata: Tunicata	*Botrylloides violaceus* (=*aurantius*)	5, 6	This study	X	X	
	Molgula manhattensis	5, 6	This study	X	X	X
	Styela clava[b]		Carlton, 1979	X	X	X

Table 1 (*continued*)

Taxon	Species	Sites	Reference	Transport
				OC SF BW
Cryptogenic invertebrates				
Porifera	*Haliclona* spp.	5, 9	This study	
	Topsentia sp.[c]	5	This study	
Cnidaria: Hydrozoa	*Obelia* spp.	2–5, 9	MacGinitie, 1935; this study	
Arthropoda: Pycnogonida	*Ammothea hilgendorfi*[c]	5, 9	Nybakken et al., 1977; this study	
Bryozoa	*Buskia seriata*[c]	5	This study	
Chordata: Tunicata	*Didemnum ?carnulentum*	6	This study	

[a] The first and second columns list taxa and species. The third column lists our collection sites; numbers correspond to Fig. 1. The fourth column lists selected references to the presence of the species at ES; we have listed only the first reference, our study (if we found it), and thorough reviews. The fifth through eighth columns list the main transport mechanisms with which the exotic species are likely to be associated (in general, not specifically for ES); except for species marked with [c], this was taken from Cohen and Carlton (1995). Abbreviations for transport mechanisms are as follows: OC, oyster culture; SF, ship fouling, BW, ballast water.

[b] Species that are conspicuous enough to be noticed in surveys, but were not found in recent decades and are assumed to be locally extinct.

[c] Species that are not known from San Francisco Bay.

In our field searches, we did not find all the exotic species that had previously been reported for ES. This is hardly surprising, as we did not search the infaunal habitats on which most previous authors had focused, and since many species are patchy or rare. Many of these earlier reported species that we did not collect are likely still present at ES. However, at least five of the exotic species reported in the past from ES appear no longer to be present, or at least have become extremely rare. These five are the gastropod *Urosalpinx cinerea*, the bivalves *Musculista senhousia* and *Mya arenaria*, the sponge *Cliona celata* and the ascidian *Styela clava*. They are conspicuous animals that should have been revealed by our surveys; indeed, we actively searched for them. Another local zoologist also confirms he has not encountered them during frequent field surveys in the past decade (J. Nybakken, personal communication).

4. Discussion

4.1. Elkhorn Slough: a highly invaded estuary

We were astonished to document over 50 exotic invertebrates at ES, especially considering the comparatively modest scale of our study (only 50 person-hours of search effort in the field). To our knowledge, this is by far the largest number of exotic invertebrates recorded for an estuary without international shipping. Moreover, Fig. 2 strongly suggests that there are many more exotic species left to find at ES; we have not yet reached a decline in the discovery of new invaders.

Of the 56 invaders documented from ES, 51 have also been reported from SFB (Cohen and Carlton, 1995); five invaders (the sponge *Hymeniacidon ?sinapium*, the snail *Batillaria attramentaria* and its trematode parasite *Cercaria batillariae*, the amphipod *Corophium uenoi*, and the bryozoan *Amathia vidovici*) are known from ES but not SFB. Conversely, 78 of the exotic species found at SFB have not yet been reported from ES. There is no significant difference between ES and SFB in origin of invaders (Table 2). The majority of invaders in ES as in SFB are native to the north Atlantic, and most of the rest hail from the western Pacific. How did the exotic species at ES get from their distant native waters to this relatively isolated estuary?

Table 2
Origin of exotic species found in Elkhorn Slough and San Francisco Bay[a]

Invaders in	Origin of invaders			
	North Atlantic	Western Pacific	Other	Total
Elkhorn Slough	26 (52)	21 (42)	3 (6)	50
San Francisco Bay	59 (56)	39 (37)	7 (7)	105

[a] Based on Cohen and Carlton (1995); invaders whose origins are uncertain were excluded from the analysis. Number of species found is followed by percentage in parentheses. There was no significant difference in the patterns for the two sites ($P=0.84$, $\chi^2=0.34$).

4.2. Routes of introduction

4.2.1. Oyster culturing

Undoubtedly, many exotic invertebrates arrived at ES with cultured oysters, a well-known mechanism of introduction (e.g. Carlton, 1979; Ruiz et al., 1997). Atlantic oysters (*Crassostrea virginica*) and Asian oysters (*Crassostrea gigas*) were repeatedly planted at ES from the turn of the century to the 1970s, with the peak of activity in the 1930s and 1940s (Carlton, 1979; Caffrey et al., 2001). Oysters from Mexico (*Ostrea corteziensis* or *Ostrea iridescens*) were tried in 1929, but

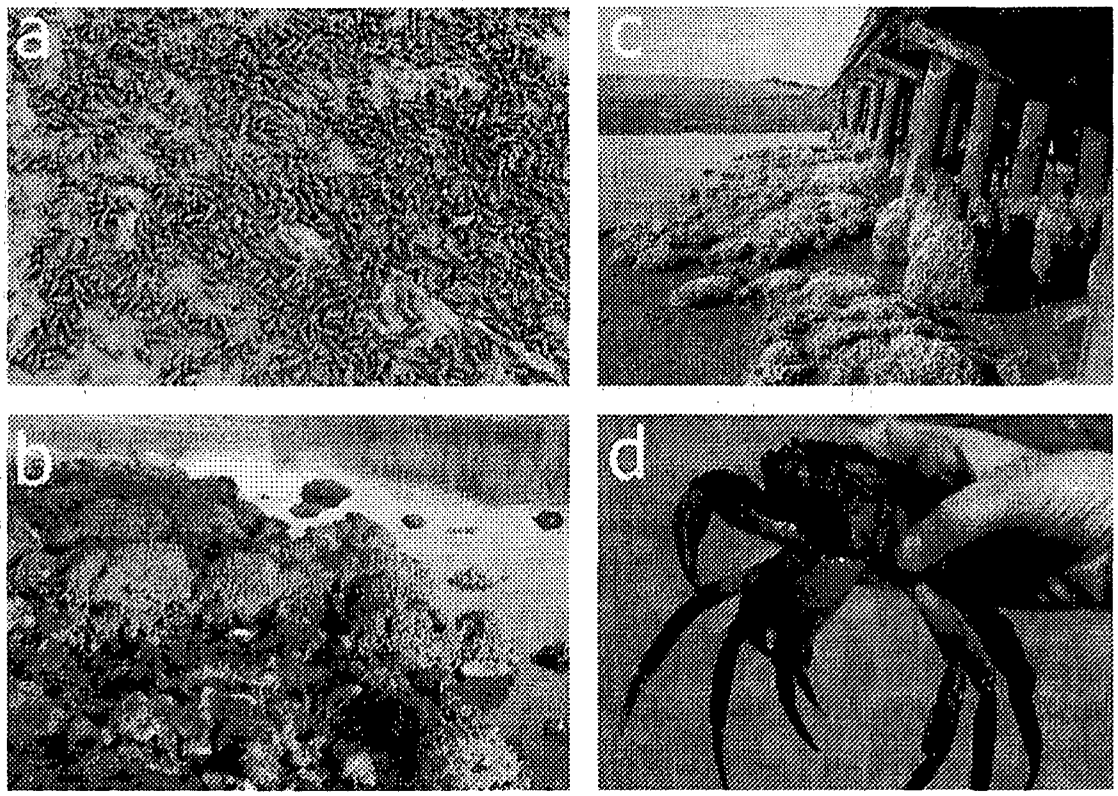

Fig. 4. Conspicuous invaders at Elkhorn Slough: (a) a high density aggregation of *Batillaria attramentaria*, the Japanese mud snail; (b) abundant masses of *Hymeniacidon ?sinapium*, an orange sponge; (c) reefs formed by *Ficopomatus enigmaticus*, the Australian tubeworm; (d) *Carcinus maenas*, a large European green crab.

failed to survive (Bonnot, 1935a). The European oyster (*Ostrea edulis*) was briefly grown in ES in the 1960s (Carlton, 1979). In addition to direct transport of oysters from their native bioregions to ES, oysters were likely brought in from other regional bays (e.g. Newport, San Francisco, Humboldt); such transfers of oysters between growers in different bays are routine, but rarely well documented (J. Carlton, personal communication). Most oyster culturing stopped in ES by the 1960s due to concern over unsafe levels of coliform bacteria; the last commercial operations ceased in the early 1980s (Caffrey et al., 2001).

Overall, 38 exotic invertebrates found at ES have the potential to be transported with oysters (Table 1) and may have been introduced to ES by this mechanism, although many are also associated with other transport mechanisms. (Ironically, this list does not include any of the four oyster species themselves; oysters never became established at ES, while many species unintentionally transported with them did.) While about two-thirds of exotic species found in ES are potentially associated with oysters, only about half of those found only in SFB are (Table 3A). This significant difference suggests that oyster culturing was relatively more important as a mechanism of introduction for ES than SFB.

Two examples illustrate the role of oyster-associated introductions at ES. The Japanese mud snail (*Batillaria attramentaria*) was likely introduced with Asian oysters in the 1920s or 1930s; it was detected in a shipment of Asian oyster spat sent to ES in 1929 (Bonnot, 1935b). This species is now easily the most abundant macroscopic animal species at ES (Fig. 4a). Based on densities measured by Byers (1999), we estimate that upwards of 10^9 Japanese mud snails are living in ES! This exotic can outcompete a similiar native snail, *Cerithidea californica*, due to more efficient conversion of resources into growth, lighter parasite loads, higher dispersal rates, and better tolerance of hypoxia (Byers, 2000a–c). The Japanese mud snail, found on this coast only at estuaries with a history of oyster culturing, is gradually displacing the native species in areas where they co-occur (Byers, 1999).

A second example is the sponge *Hymeniacidon ?sinapium*, one of the most conspicuous creatures in upper ES (Fig. 4b), which forms massive, bright orange balls with frilly protrusions. In addition to occurring on or near hard substrate such as gravel bars or drainage pipes, healthy individuals are found unattached on mud, an unusual habitat for sponges. This species was described by de Laubenfels (1930), who found it to be

Table 3
Comparison of potential transport mechanisms of exotic species for Elkhorn Slough and San Francisco Bay[a]

Invaders in	Yes	No	Total
(A) Oyster culture a potential transport mechanism			
Invaders in			
Elkhorn Slough	38 (68)	18 (32)	56
San Francisco Bay	63 (49)	66 (51)	129
(B) Oyster culture or ship fouling a potential transport mechanism			
Invaders in			
Elkhorn Slough	53 (95)	3 (5)	56
San Francisco Bay	103 (80)	26 (20)	129

[a] (A) Exotics associated with oyster culture. Yes, oyster culture is included as a possible transport mechanism for species in Table 1; No, it is not. (B) Exotics associated with either oyster culturing or ship fouling. Yes, oyster culture *or* ship fouling are listed as possible transport mechanism for species in Table 1; No, neither oyster culture or ship fouling listed as a possible transport mechanism. Number of exotic species is followed by percentage, in parentheses. A chi-square test revealed that patterns differed significantly between the two groups for both comparisons; for (A) $P=0.02$, $\chi^2=5.70$; for (B) $P=0.01$, $\chi^2=6.47$.

very abundant in beds of Atlantic oysters in Newport Bay and other southern Californian bays (de Laubenfels, 1932); we therefore postulate the species was introduced to ES with oysters. (*H. sinapium* is probably a junior synonym of *Hymeniacidon caruncula* or another Atlantic species; the genus comprises a number of very similar, likely synonymous species, and is in need of taxonomic revision.) The abundant orange sponge at ES may be influencing community composition, by its vigorous filtering activities, and by providing firm substrate in soft-bottom habitats.

4.2.2. Fouling on boats and ships

Besides oyster culturing, the other major mechanism likely to be responsible for introducing exotic species to ES is ship fouling. Most exotic species in ES (70%) are associated with ship fouling (Table 1), and therefore, could readily have been transported to ES on boats that picked up fouling species on their hulls while anchored in areas with abundant established populations of invaders. Boat traffic between Moss Landing (at the mouth of ES) and other regional harbors has a long history, and frequent voyages between Moss Landing and San Francisco have been documented at least as far back as the mid-1800s (Silberstein and Campbell, 1989). Today, boat traffic between Moss Landing and other local ports continues to be common (S. Schieblauer, Monterey Harbormaster, personal communication; J. Stilwell, Moss Landing Harbormaster, personal communication). The 600 or so resident fishing and pleasure boats mostly travel short distances up and down the coast. For instance, many fishing boats from the Monterey Bay region travel annually to the SFB area to catch herring, and when fishing is poor or weather bad, often remain there for long periods before returning to Moss Landing. There is also an annual migration of fishing boats along the coast, bringing a temporary influx of boats to Monterey Bay from other regional harbors as far south as Baja California, Mexico, and from as far north as Alaska (S. Schieblauer, personal communication). In contrast to the lively regional boat traffic, very few if any boats arrive at Moss Landing Harbor directly from distant seas.

The burrowing isopod *Sphaeroma quoyanum* illustrates the role of ship fouling at ES. Originally from Australia and New Zealand, *S. quoyanum* was first reported in SFB in 1893. It rapidly spread throughout California bays and harbors, almost certainly via ship fouling (Cohen and Carlton, 1995). The burrows of this isopod riddle virtually every bank we examined at ES, perhaps exacerbating already high rates of tidal erosion (S. Stout Bane, in preparation). Accompanying this invader at ES, as at SFB (Cohen and Carlton, 1995), is a tiny commensal isopod, *Iais californica*, which clings to *Sphaeroma*'s ventral surface. The role of commensals such as this species, of parasites (such as the trematode *Cercaria batillariae* that accompanied the Japanese mud snail to ES), and of mutualists in shaping estuarine invasion success is mostly unexplored.

4.2.3. Other mechanisms of introduction

Oyster culturing and ship fouling can account for almost all introductions to ES; of the 56 exotic species found ES and SFB, only three (5%) are not associated with either ship fouling or oysters (Table 3B). In contrast, significantly more (20%) of the exotic species found only in SFB are associated exclusively with other transport mechanisms (Table 3B). In particular, ballast water dumping is considered to be responsible for the majority of recent introductions to SFB (Cohen and Carlton, 1995) and to other large estuaries around the world (Carlton, 1985; Ruiz et al., 1997). Large international vessels with extensive ballast tanks very rarely dock at Moss Landing Harbor (J. Stilwell, personal communication), or even enter the Monterey Bay area (S. Shieblauer, personal communication), so ballast water discharge is not an important mechanism of introduction to ES.

Besides oyster culturing and boat traffic, a variety of other mechanisms could potentially introduce exotic species to ES. These include intentional introductions for fisheries, aquaculture, or biocontrol efforts, and unintentional transport with seaweed used to pack bait or seafood. For instance, the soft-shell clam *Mya arenaria* is known to have been planted in Santa Cruz and Tomales Bay (Hanna, 1939) and might also have been intentionally introduced to ES. Another such example comes from the planting of native eelgrass (*Zostera marina*) from various West Coast embayments (e.g. Coos, Humboldt, Tomales Bays) in ES in 1990; plants were transplanted in a matrix of surrounding sediment that could have included some of the exotic species established in these places. Such introductions are probably rare events and have been found to account for only a small percentage of invaders in SFB (Cohen and Carlton, 1995). We suspect that due to lower human activity levels at ES, these types of introductions are even less common there.

4.3. *The importance of intraregional transport*

4.3.1. *Spread between vs. within regions*

The initial invasion of a new region by an exotic species occurs, by definition, by *inter*regional mechanisms. Worldwide, international vessels and cultured oysters arriving directly from distant waters are the most common culprits, inadvertently transporting exotic species between regions (Carlton, 1985; Ruiz et al., 1997). The movement of vast volumes of water in ballast tanks of international vessels has been singled out as the most important current source of new estuarine invasions (National Research Council, 1996). Focus on such interregional mechanisms responsible for invasions has understandably resulted from investigations of large estuaries such as SFB, where international shipping (fouling on hulls and ballast water) is considered responsible for most recent introductions (Cohen and Carlton, 1995).

After an exotic species initially invades a new bioregion and becomes established, it may spread within the region by *intra*regional mechanisms including boat traffic, exchange of oyster stock by growers in different bays, and natural dispersal of larvae on currents (Zevina and Kuznetsova, 1965; Bell et al., 1987; Geller, 1994). Such routes of transport are likely to be very important for invasions of ES and other small estuaries. The 18 exotic species not associated with oyster-culture (Table 3a), the only significant interregional transport mechanism for ES, must have arrived via intraregional spread. Indeed, many of the remaining 38 ES species that are associated with oysters may have been transported intraregionally as well, since oysters were transferred between bays, and since most of these species are also associated with other intraregional mechanisms such as ship-fouling (Table 1). Furthermore, intraregional spread must account for the new invasions of ES that have apparently continued unabated (Fig. 3) in the decades following the decline and cessation of oyster culturing. Intraregional transport mechanisms have received little attention in the published literature, and yet our results suggest that they are critical to a full understanding of the phenomenon of estuarine invasions.

4.3.2. *International ports as stepping stones for invaders*

Due to their heavy exposure to *inter*regional transport mechanisms, large estuaries with international shipping become sources for *intra*regional spread. SFB, with its rich exotic fauna, likely plays an especially important role as a source of exotic species arriving at ES. Invaders at ES appear to be a nested subset of SFB exotic species: 51 of the 56 exotic ES species are found in SFB. A χ^2 contingency analysis showed that these 51 species are not a random subset of the 129 marine invertebrate invaders found in SFB, but instead disproportionately represent those species with access to intraregional transport mechanisms. Only 3/51 (6%) of SFB species shared with ES were not associated with ship-fouling or oyster culture. In contrast, a far greater proportion (23/78 = 29%) of species limited to SFB was not associated with these two mechanisms. This highly significant ($P=0.001$, $\chi^2=10.68$) difference suggests that SFB exotics with access to intraregional transport are the source of many invasions of ES.

Three examples of recent invasions of ES illustrate how SFB can act as a stepping stone for exotic species. The Australian reef-forming tubeworm (*Ficopomatus enigmaticus*), the European green crab (*Carcinus maenas*), and the western Pacific tortellini snail (*Philine auriformis*) all invaded SFB by interregional transport before spreading along the coast. The tubeworm likely arrived at SFB fouling an international ship. Reefs of this worm were first noted in SFB in 1920 (Cohen and Carlton, 1995). Over 70 years later, it was first reported at ES, by a student (J. Alicea) in an unpublished class report (Moss Landing Marine Laboratories, Marine Ecology, 1994). Alicea found extensive reefs only in one area in the lower Slough system (site 1, Fig. 1); no reefs were found in the upper Slough (sites 9–10) despite thorough searches. Five years later, we found extensive reefs at site 10, and smaller patches at site 9. The tubeworm is known from nowhere else on this coast besides SFB and now ES; it seems to spread very slowly by intraregional transport, likely via fouling on regional boats. Once the worm is introduced and established, however, it can become locally dominant. Vast reefs now cover hard substrate in parts of ES (Fig. 4c), and the distribution of the worm in this estuary is probably still expanding.

The European green crab (Fig. 4d) has only recently become established in western North America. Juvenile green crabs are found among the algae used as packing material for bait and seafood sent from the Atlantic coast, where the species is abundant, so this route of transport seems mostly likely for its introduction (Cohen and Carlton, 1995). First noted in SFB in about 1989 (Cohen et al., 1995), the crab has undergone a remarkably rapid range expansion to the north and south (Grosholz and Ruiz, 1995). Green crab individuals have been reported from as far north as Vancouver, BC (A. Cohen, personal communication) and as far south as Morro Bay, CA (E. Grosholz, personal communication). At Bodega Harbor in northern California, this crab has been shown to greatly reduce populations of native bivalves and crustaceans (Grosholz and Ruiz, 1995; Grosholz et al. 2000), and it may pose a threat to commercially important species such as oysters, clams, and dungeness crab (*Cancer magister*) on the west coast. The green crab first appeared in ES in 1994 (Grosholz and Ruiz, 1995). Not known to be associated with boat traffic, green crabs probably spread to ES and elsewhere along the coast via natural larval transport on currents. A southward current runs along this region of coast from about March to July, such that a larva could be passively transported the 150 km from SFB to ES within a few weeks (Paduan and Rosenfeld, 1996); Grosholz (1996) calculated that larval transport could easily account for the rate of spread of the green crab along this coast.

Likewise, the tortellini snail probably spread to ES from SFB by transport of larvae on currents. Tortellini snails were first observed in SFB in 1992, most likely transported via ballast water, and were soon afterwards seen in Bodega Harbor, to the north (Gosliner, 1995). Voracious predators on bivalves, tortellini snails have the potential to profoundly impact benthic communities. By 1995, the tortellini snail was abundant in channels in ES (J. Engel, personal communication). All three of these examples illustrate that intraregional spread can occur by different mechanisms, and in separate events, than interregional transport.

4.3.3. Preventing future intraregional invasions

Invasive marine invertebrates are difficult, if not impossible, to eradicate once well-established and widespread. New colonizations can perhaps be removed to prevent establishment, but such efforts would require early detection of invasions. Unless the biota of estuaries such as ES is regularly monitored, such early detection is not possible. The other key management strategy is of course to focus on prevention. As a rule, the more propagules (adults, larvae, spores, or seeds) of an exotic species that arrive in an area, the more likely it is to become successfully established, given physical suitability of the new location (Williamson, 1996). We recommend two approaches to reduce the influx of invasive propagules to estuaries such as ES.

One management approach is to decrease regional source populations of invaders. Every new species that arrives and becomes established at SFB has the potential to subsequently spread. So policies limiting *inter*regional transport, such as ballast water treatment regulations, translate into fewer new *intra*regional invasions. The importance of limiting interregional mechanisms, particularly those associated with international shipping, has recently gained significant recognition (e.g. National Research Council, 1996), although the indirect benefits to estuaries without international shipping have not been emphasized.

A second management approach is to directly limit intraregional transport mechanisms. There is nothing that can be done to stop the natural diffusive spread of species, for instance by larvae travelling on currents. However, as our results show, anthropogenic transport is responsible for many transfers of exotic species between estuaries. Mechanisms for reducing transport due to all of the human-related mechanisms discussed above can be readily envisioned. Hulls of boats can be scrubbed after prolonged visits to major harbors, and contents of live wells could be discharged into treatment facilities. Bait and its algal packing material could be disposed of into garbage containers. Oysters and other aquaculture organisms could be thoroughly cleaned before being exchanged between bays. Such measures have received little attention, and would require substantial educational efforts, and perhaps regulatory policy, in order to be effectively implemented.

4.3.4. Developing a predictive approach to intraregional invasions

For predictions about new invasions and for control of existing ones, an understanding of the processes that underlie successful vs. failed invasions is essential. A better theoretical framework is needed for intraregional invasions. Based on our results, we suggest that two areas will be particularly fruitful. First, it is important to examine intraregional dispersal mechanisms to identify which species have access to transport mechanisms and are thus likely to become introduced to multiple estuaries. The significant difference we found in transport mechanisms for SFB species that did vs. did not invade ES suggests that dispersal opportunity is one good predictor of estuarine invasion. The 23 species found only in SFB that are not associated with oysters or ship fouling simply had less opportunity to invade ES. Second, we need a better understanding of the causes of local extinctions of populations of invaders following initial successful establishment. In ES, at least five conspicuous invasive species that were once established are now absent or at least so rare that they were not found in our fieldwork. Determining whether competition, predation, or parasitism by native species, say, or perhaps episodic challenging physical conditions led to the demise of these populations would provide valuable insights for controlling other invaders and for restoring native habitats in such a way as to minimize future invasions. The theory of island biogeography (MacArthur and Wilson, 1967), with its focus on local colonizations and extinctions, might serve to characterize the community dynamics of invasions within a region. Almost all of the exotic invertebrates reported from the northeastern Pacific coast are found in bays and estuaries, not along the open coast, so the metaphor is ecologically apt, with isolated "islands" of estuarine habitat along the coast. Comparisons of fauna among multiple embayments would allow more rigorous examination of the influence of major ports on nearby bays and estuaries. Important questions include the role of size (do large bays have more exotic species than small ones, and is this due to higher colonization rates, or lower extinction rates?) and distance (do nearby estuaries have a more similar exotic fauna than distant ones?). For understanding the population dynamics of single invaders, metapopulation models and their variants (Harrison, 1991) might be relevant for examining patterns of local extinction and re-colonization due to migration between estuaries. Future studies that test hypotheses based on such models will allow us to better predict the patterns and consequences of intraregional invasions.

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Biological invasions of estuaries without international shipping: the importance of intraregional transport

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Abstract

Increased awareness of the problem of introduced marine species has led to recent surveys of several large bays with international shipping. To our knowledge, no thorough search for introductions has been carried out in an embayment *not* connected to an international harbor. In 1998, we investigated the macroinvertebrate fauna of Elkhorn Slough (ES), an estuary in central California. Fieldwork and a literature review revealed 56 known exotic species at ES, a surprising diversity considering the rather modest search effort, the relatively natural setting of this estuary, and the lack of international shipping. While some exotic species at ES were probably introduced directly from distant waters with cultivated oysters, others likely arrived more indirectly via San Francisco Bay or other regional ports with thriving populations of invaders, travelling for instance as adults fouling boats or as larvae on currents. The effect of international shipping, including ballast water dumping, is thus not limited to areas with major harbors, but rather reverberates up and down the coast to seemingly isolated embayments.

Keywords: Biological invasions; Exotic species; Elkhorn Slough; Ballast water; Invertebrates

1. Introduction

Exotic marine organisms are ubiquitous in bays with large harbors supporting intensive international shipping. For example, about 150 nonindigenous invertebrates have been documented in San Francisco Bay, California (Cohen and Carlton, 1995), 100 in Pearl Harbor, Hawaii (Coles et al., 1997), 50 in Puget Sound, Washington (Cohen et al., 1998), and 100 in Port Phillip Bay, Australia (Hewitt et al., 1999). These invaders arrived by various means, including aquaculture and ship-hull fouling. Recently, however, the most significant mechanism of introduction has been ballast water (Carlton, 1985; Ruiz et al., 1997), which is pumped and gravitated into vessels at one port, and discharged at another, transporting planktonic and nektonic organisms (as well as benthic organisms in sediments inadvertently taken in with the water) between regions. As a result of these human-mediated introductions, the fauna of many harbor areas has become homogenized as native species are reduced in abundance and habitat breadth (Ruiz et al., 1997).

The problem of invasions in major harbors and associated bays is gaining increasing recognition, but the degree to which the problem also exists in small bays with little or no international shipping is not well known. Are invaders also diverse and abundant in the smaller estuaries and bays that lie between major shipping ports? In the northeastern Pacific region, some exotic species have been identified and studied in smaller embayments (e.g. Carlton, 1979; Grosholz and Ruiz, 1995; Byers, 1999), but few if any systematic broad-scale, multi-taxon searches have been carried out in such places. Since direct transport from distant waters via international ship fouling or ballast water is uncommon at such embayments, the diversity of invaders might be lower. However, exotic species may become established at smaller embayments through other direct mechanisms, such as culturing of oysters

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brought in from other regions. Exotic species may also arrive indirectly via intraregional transport; in particular, invaders introduced to a major port by shipping may spread along the coast once established (Cohen and Carlton, 1995; Grosholz and Ruiz, 1995; Hewitt et al., 1999). Such secondary transport may occur by natural mechanisms such as movement of adults or larvae, or by anthropogenic mechanisms such as exchange of commercial oyster stocks by growers in different bays or travel between harbors by boats carrying organisms on their hulls or in their live-well water.

We investigated the exotic invertebrate fauna at Elkhorn Slough (ES), California, an estuary about 150 km south of San Francisco Bay (SFB). ES has had a long history of oyster culture, now abandoned, and there is a small harbor for fishing and recreational boats at its mouth. We compared the exotic fauna of ES to that of SFB (1) to determine whether the absence of international shipping and particularly ballast water dumping has protected ES from being as severely invaded as SFB, and (2) to explore whether the proximity of SFB with its well-established populations of exotic species has affected the species composition of ES.

2. Methods

2.1. Characterization of Elkhorn Slough

Elkhorn Slough (ES) is a large coastal wetland located in central California, just inland of Moss Landing Harbor at the midpoint of the Monterey Bay (Fig. 1). Its history, biology, and physical setting have been well characterized (Schwartz et al., 1986, Silberstein and Campbell, 1989, Caffrey et al., 2001). Drainage from the old Salinas River channel (site 1, Fig. 1) supplies freshwater year-round near Moss Landing (site 2) at the mouth of the slough. The upper reaches of ES (e.g. site 10) are sometimes hyposaline in the rainy season and sometimes hypersaline in the dry season. However, freshwater input to ES is minor compared to the tidal prism, and the majority of ES wetland habitats are essentially marine due to strong tidal flushing, especially along main channel (e.g. sites 4, 8, 9). Water quality is influenced by runoff from adjacent farmlands; extremely high nutrient, pesticide, and coliform bacterial levels have been documented. About 500 native species of marine invertebrates have been reported from ES (Caffrey et al., 2001).

2.2. Collection, identification, and categorization of invertebrates

We searched intensively for invertebrates at ten intertidal sites at ES (Fig. 1) during two consecutive low spring tides in March, April, May and July 1998. We estimate that about 10 person-hours were spent searching during each of these four sampling periods. In the subsequent 2 years, we occasionally searched for invertebrates; we estimate that about 10 additional hours were spent searching in these later miscellaneous efforts. Therefore, the total field search effort for this study sums to 50 person-hours.

At each site, we looked for any intertidal or shallow subtidal invertebrates we could find, usually focusing on organisms on rocks, pilings, or other available hard substrates, since an extensive previous study (Nybakken et al., 1977) had rigorously investigated the infaunal community of ES. We collected specimens of all species we did not confidently recognize as natives. The specimens were microscopically examined at Long Marine Laboratory in Santa Cruz, and were identified using Light's Manual (Smith and Carlton, 1975) and additional references from the primary literature when necessary. Difficult specimens were sent to taxonomic experts for identification. We deposited voucher specimens of all exotic and cryptogenic species we collected in the California Academy of Sciences (catalogue numbers 144150-144188).

In addition to this fieldwork, we carried out a literature review for exotic species at ES. We looked for the first reference to the presence of each exotic species, which often originated from MacGinitie's (1935) classic work at ES or from Nybakken et al. (1977). From our fieldwork and literature search, we complied a list of exotic invertebrates (Table 1), mostly using the designations

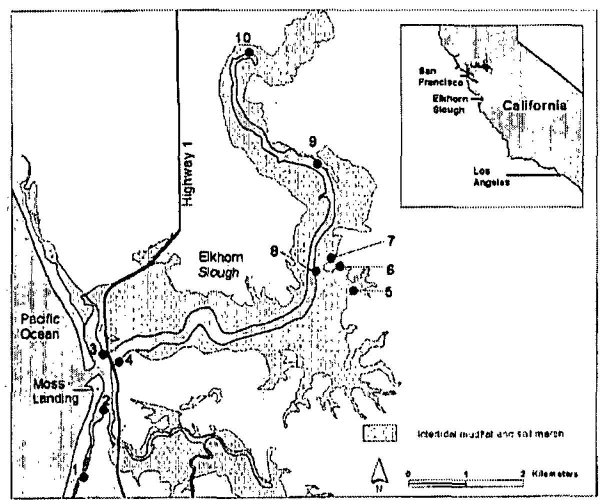

Fig. 1. Location of collection sites at Elkhorn Slough, California. Numbering of sites corresponds to Table 1. The exact location of these sites is as follows: 1, north side of bridge over old Salinas River channel, just south of Moss Landing; 2, Moss Landing Harbor; 3, "Skipper's", just northwest of Highway 1 bridge; 4, "Vierra's", just southeast of Highway 1 bridge; 5, area around footbridge on South Marsh trail; 6, Whistlestop Lagoon, 7, "Batillaria Heaven", mud pan on Hummingbird Island; 8, main channel of Slough at shore of Hummingbird Island; 9, Kirby Park, near boat ramp; 10, Hudson's Landing, just west of Elkhorn Road.

of previous authors (especially Smith and Carlton, 1975; Cohen and Carlton, 1995) to determine whether a species was native to the northeastern Pacific. For species not listed in these references, we made our own determinations as follows: species with very disjunct global distributions, not previously recorded at ES and described originally from distant localities, were considered exotic, while those with somewhat disjunct or cosmopolitan distributions were considered cryptogenic (*sensu* Carlton, 1996: a cryptogenic species is one whose origin cannot readily be determined with available data). We examined patterns of invasion over time for all ES exotic species, and assessed native ranges and likely transport mechanisms for each species based on the literature, relying heavily on determinations made by Cohen and Carlton (1995).

2.3. Comparison to San Francisco Bay (SFB)

We compared our exotic species list for ES to that of Cohen and Carlton (1995) for SFB. For the purposes of this comparison, we omitted 16 SFB species (from their list of 147 invertebrates) that are limited to freshwater habitats, which are absent from ES. We also eliminated from the analysis three species-complexes (the jelly *Aurelia aurita*/*Aurelia* sp.; the hydroid *Obelia* spp.; the clam *Macoma balthica*/*Macoma petalum*) found in both studies. These complexes each consist of native and exotic species that are so morphologically similar that they cannot readily be distinguished without molecular methods.

We compared species richness and species composition of exotic invertebrates between ES and SFB. To determine whether there were differences in origins of invaders, we used a χ^2 contingency analysis to compare native ranges of the total exotic species found in ES vs. SFB. To compare frequency of different transport mechanisms for the two estuaries, we carried out two χ^2 contingency analyses for ES vs. SFB invaders. To determine whether species found only in SFB were associated with different transport mechanisms than those also found in ES, we used another χ^2 contingency analysis to compare transport mechanisms of exotic species found *only* in SFB (not ES) vs. those found in *both* SFB and ES.

3. Results

A total of 56 exotic invertebrate species are now known from Elkhorn Slough (Table 1). In our fieldwork, we collected 34 exotic species and six cryptogenic species. Of these, 19 of the exotic and four of the cryptogenic species had not previously been reported for ES. We found nearly half of these previously unreported species during our first sampling period in March 1998, and the rest spread fairly evenly between April, May, and July 1998 and miscellaneous later efforts (Fig. 2). On average, we collected about one previously unreported species for every 2 h of search effort. Our literature review revealed 16 additional exotic species reported for ES. We also learned of six invaders found by others at ES but never reported in the literature (listed as personal communications in Table 1).

It is difficult to determine when each of these 56 species first became established at ES. Fig. 3 shows the number of new invaders at ES per year reported in published literature. The largest peaks are in 1935, 1977, and 2001, representing MacGinitie's, Nybakken et al.'s, and our studies, respectively. The new species reported by each study were likely present well before publication, so this graph cannot be read as an accurate representation of the specific timing of invasions. However, the general temporal trends are probably reliable; invasions have occurred continuously over this whole period, certainly without a decline, and perhaps even with an increase over time.

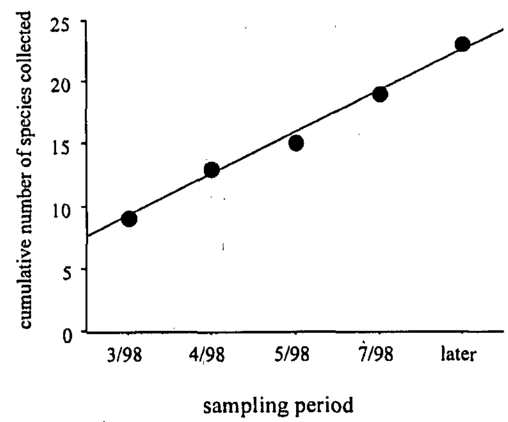

Fig. 2. Cumulative number of previously unreported exotic and cryptogenic species collected at Elkhorn Slough in the current study, by sampling period. About 10 person hours were spent searching in the field during each period. A linear regression model provides an excellent fit to the data ($R^2=0.99$, $P=0.0004$), indicating that the cumulative number of new species collected increased consistently with net search effort.

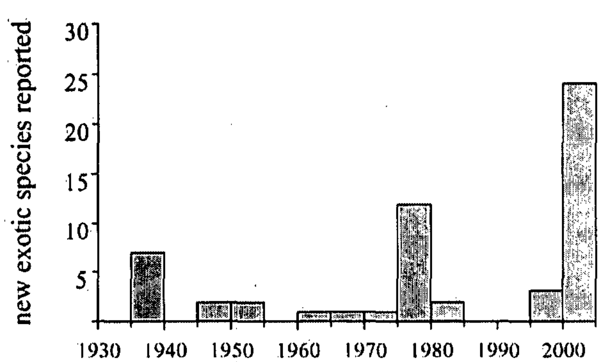

Fig. 3. Number of new exotic species reported in the literature for Elkhorn Slough each year.

Table 1
Exotic and cryptogenic species of Elkhorn Slough[a]

Taxon	Species	Sites	Reference	Transport		
				OC	SF	BW
Exotic invertebrates						
Porifera	*Cliona celata*[b]		Nybakken et at., 1977	X		
	Halichondria bowerbanki	5, 6, 9	MacDonald and Nybakken, 1978; this study	X	X	
	Haliciona ?loosanoffi	4–6, 9	This study	X	X	
	Hymeniacidon ?sinapium[c]	5, 6	This study	X	X	
Cnidaria: Hydrozoa	*Cordylophora caspia*	1	This study		X	X
	Ectopleura crocea	3–5, 9	MacGinitie, 1935; Canton, 1979; this study	X	X	
Anthozoa	*Diadumene franciscana*	5	This study		X	X
	Diadumene leucolena	4, 7	This study	X	X	X
	Diadumene lineata	4, 5, 7, 9	Ricketts and Calvin, 1939; Carlton, 1979, this study	X	X	
Platyhelminthes: Trematoda	*Cercaria batillariae*[c]		J. Byers, personal communication	X		
Annelida: Polychaeta	*Ficopomatus enigmaticus*	1, 9, 10	J. Alicea. personal communication, this study		X	
	Heteromastus filiformis		Nybakken et al., 1977	X		X
	Polydora ligni		Carlton, 1979	X	X	X
	Pseudopolydora paucibranchiata		Blake and Woodwick 1975; Carlton 1979	X	X	X
	Streblospio benedicti	5, 9	Blake and Woodwick, 1975; Carlton, 1979; this study	X	X	X
Mollusca: Gastropoda	*Urosalpinx cinerea*[b]		Burch, 1945b; Smith and Gordon, 1948; Carlton 1979	X		
	Batillaria attramentaria[c]	1 – 10	McLean, 1960; Carlton, 1979; Byers, 1999; this study	X		
	Okenia plana	9	This study	X	X	X
	Philine auriformis	8	This study			X
	Tenellia adspersa	9	Carlton 1979; this study		X	X
	Myosotella myosotis	2	Burch, 1945a; Carlton, 1979; this study	X	X	
Bivalvia	*Gemma gemma*	5, 9, 10	MacDonald, 1969; Carlton, 1979; this study	X		
	Lyrodus pedicellatus		MacGinitie, 1935; Carlton, 1979		X	
	Musculista senhousia[b]		Carlton, 1979	X		
	Mya arenaria[b]		MacGinitie, 1935; Carlton, 1979	X		
	Mytilus galloprovincialis	1–6, 9	Suchanek et al., 1997; this study		X	X
	Venerupis philippinarum	4	Shaw, 1950; Carlton, 1979; this study	X		
Crustacea: Copepoda	*Mytilicola orientalis*		Katkansky and Warner, 1974; Carlton, 1979	X		
Cirripedia	*Balanus improvisus*	4, 5	This study	X	X	
Tanaidacea	*Sinelobus* sp.		P. Slattery, personal communication		X	X
Isopoda	*Iais californica*	5, 6, 9	This study		X	
	Limnoria quadripunctata		MacGinitie, 1935; Carlton, 1979		X	
	Sphaeroma quoyanum	1, 5, 6, 9, 10	This study		X	
Amphipoda	*Ampithoe valida*		P. Slattery, personal communication	X	X	X
	Caprella mutica		Marelli, 1981; Cohen and Carlton, 1995	X		X
	Corophium acherusicum		Nybakken et al., 1977; Carlton, 1979	X	X	
	Corophium insidiosum		Nybakken et al., 1977; Carlton 1979	X	X	
	Corophium uenoi[c]		Nybakken et al., 1977; Carlton, 1979	X		
	Grandidierella japonica	9	This study	X	X	X
	Jassa marmorata		J. T. Carlton, personal communication		X	X
	Melita nitida		Carlton, 1979; Chapman, 1988	X	X	X
	Parapleustes derzhavini		P. Slattery, personal communication		X	
Decapoda	*Carcinus maenas*	5, 6, 9, 10	Grosholz and Ruiz, 1995; this study			X
	Palaemon macrodactylus		Standing, 1981			X
Bryozoa	*Amathia vidovici*[c]	5, 6, 9	This study		X	
	Bowerbankia gracilis	3-6, 9	MacGinitie, 1935; this study	X	X	
	Bugula "neritina"	4-6, 9	This study	X	X	
	Bugula stolonifera	4, 5, 9	This study		X	
	Conopeum tenuissimum	2-6, 9	This study	X	X	X
	Cryptosula pallasiana	5, 6	This study	X	X	
	Schizoporella unicornis	3, 5, 9	Osburn, 1952; this study	X	X	
	Watersipora "subtorquata"	2 – 6	Cohen and Carlton, 1995; this study		X	
Kamptozoa	*Barentsia benedeni*	10	This study	X	X	
Chordata: Tunicata	*Botrylloides violaceus (=aurantius)*	5, 6	This study	X	X	
	Molgula manhattensis	5, 6	This study	X	X	X
	Styela clava[b]		Carlton, 1979	X	X	X

Table 1 (*continued*)

Taxon	Species	Sites	Reference	Transport		
				OC	SF	BW
Cryptogenic invertebrates						
Porifera	*Haliclona* spp.	5, 9	This study			
	Topsentia sp.[c]	5	This study			
Cnidaria: Hydrozoa	*Obelia* spp.	2–5, 9	MacGinitie, 1935; this study			
Arthropoda: Pycnogonida	*Ammothea hilgendorfi*[c]	5, 9	Nybakken et al., 1977; this study			
Bryozoa	*Buskia seriata*[c]	5	This study			
Chordata: Tunicata	*Didemnum ?carnulentum*	6	This study			

[a] The first and second columns list taxa and species. The third column lists our collection sites; numbers correspond to Fig. 1. The fourth column lists selected references to the presence of the species at ES; we have listed only the first reference, our study (if we found it), and thorough reviews. The fifth through eighth columns list the main transport mechanisms with which the exotic species are likely to be associated (in general, not specifically for ES); except for species marked with [c], this was taken from Cohen and Carlton (1995). Abbreviations for transport mechanisms are as follows: OC, oyster culture; SF, ship fouling, BW, ballast water.

[b] Species that are conspicuous enough to be noticed in surveys, but were not found in recent decades and are assumed to be locally extinct.

[c] Species that are not known from San Francisco Bay.

In our field searches, we did not find all the exotic species that had previously been reported for ES. This is hardly surprising, as we did not search the infaunal habitats on which most previous authors had focused, and since many species are patchy or rare. Many of these earlier reported species that we did not collect are likely still present at ES. However, at least five of the exotic species reported in the past from ES appear no longer to be present, or at least have become extremely rare. These five are the gastropod *Urosalpinx cinerea*, the bivalves *Musculista senhousia* and *Mya arenaria*, the sponge *Cliona celata* and the ascidian *Styela clava*. They are conspicuous animals that should have been revealed by our surveys; indeed, we actively searched for them. Another local zoologist also confirms he has not encountered them during frequent field surveys in the past decade (J. Nybakken, personal communication).

4. Discussion

4.1. Elkhorn Slough: a highly invaded estuary

We were astonished to document over 50 exotic invertebrates at ES, especially considering the comparatively modest scale of our study (only 50 person-hours of search effort in the field). To our knowledge, this is by far the largest number of exotic invertebrates recorded for an estuary without international shipping. Moreover, Fig. 2 strongly suggests that there are many more exotic species left to find at ES; we have not yet reached a decline in the discovery of new invaders.

Of the 56 invaders documented from ES, 51 have also been reported from SFB (Cohen and Carlton, 1995); five invaders (the sponge *Hymeniacidon ?sinapium*, the snail *Batillaria attramentaria* and its trematode parasite *Cercaria batillariae*, the amphipod *Corophium uenoi*, and the bryozoan *Amathia vidovici*) are known from ES but not SFB. Conversely, 78 of the exotic species found at SFB have not yet been reported from ES. There is no significant difference between ES and SFB in origin of invaders (Table 2). The majority of invaders in ES as in SFB are native to the north Atlantic, and most of the rest hail from the western Pacific. How did the exotic species at ES get from their distant native waters to this relatively isolated estuary?

Table 2
Origin of exotic species found in Elkhorn Slough and San Francisco Bay[a]

Invaders in	Origin of invaders			
	North Atlantic	Western Pacific	Other	Total
Elkhorn Slough	26 (52)	21 (42)	3 (6)	50
San Francisco Bay	59 (56)	39 (37)	7 (7)	105

[a] Based on Cohen and Carlton (1995); invaders whose origins are uncertain were excluded from the analysis. Number of species found is followed by percentage in parentheses. There was no significant difference in the patterns for the two sites ($P = 0.84$, $\chi^2 = 0.34$).

4.2. Routes of introduction

4.2.1. Oyster culturing

Undoubtedly, many exotic invertebrates arrived at ES with cultured oysters, a well-known mechanism of introduction (e.g. Carlton, 1979; Ruiz et al., 1997). Atlantic oysters (*Crassostrea virginica*) and Asian oysters (*Crassostrea gigas*) were repeatedly planted at ES from the turn of the century to the 1970s, with the peak of activity in the 1930s and 1940s (Carlton, 1979; Caffrey et al., 2001). Oysters from Mexico (*Ostrea corteziensis* or *Ostrea iridescens*) were tried in 1929, but

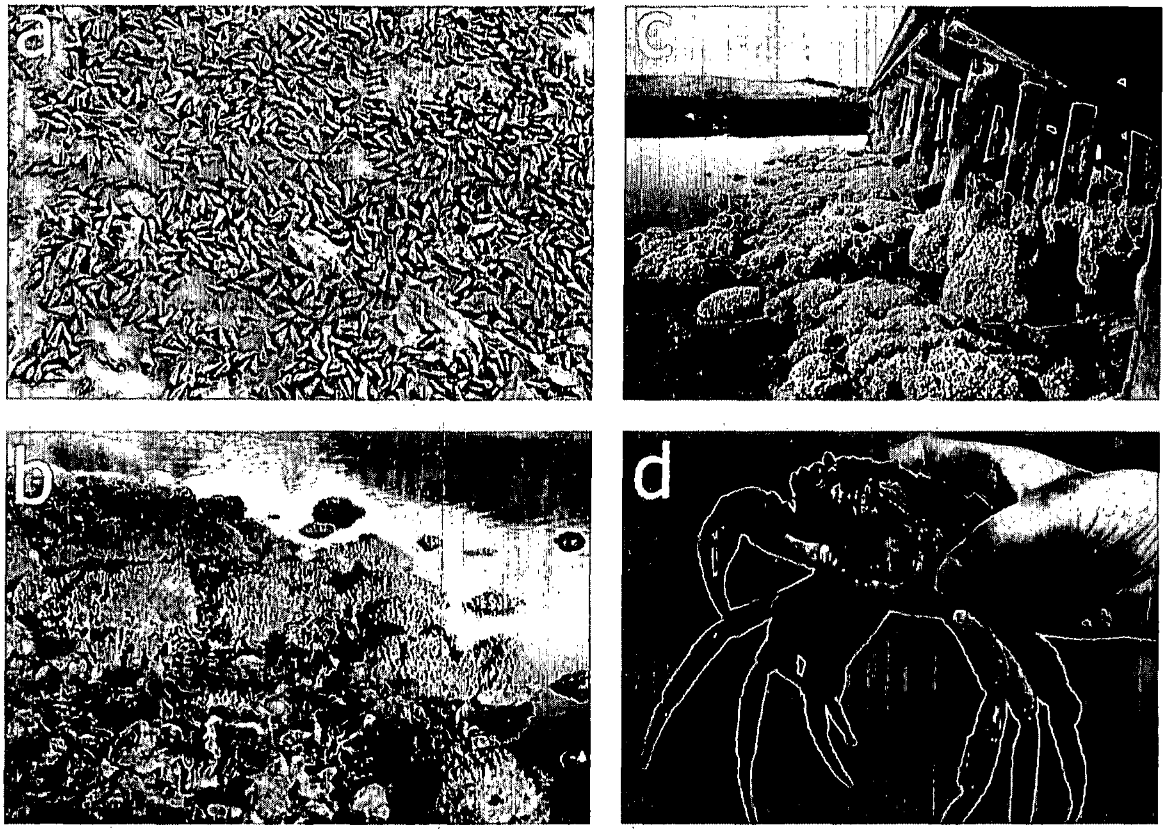

Fig. 4. Conspicuous invaders at Elkhorn Slough: (a) a high density aggregation of *Batillaria attramentaria*, the Japanese mud snail; (b) abundant masses of *Hymeniacidon ?sinapium*, an orange sponge; (c) reefs formed by *Ficopomatus enigmaticus*, the Australian tubeworm; (d) *Carcinus maenas*, a large European green crab.

failed to survive (Bonnot, 1935a). The European oyster (*Ostrea edulis*) was briefly grown in ES in the 1960s (Carlton, 1979). In addition to direct transport of oysters from their native bioregions to ES, oysters were likely brought in from other regional bays (e.g. Newport, San Francisco, Humboldt); such transfers of oysters between growers in different bays are routine, but rarely well documented (J. Carlton, personal communication). Most oyster culturing stopped in ES by the 1960s due to concern over unsafe levels of coliform bacteria; the last commercial operations ceased in the early 1980s (Caffrey et al., 2001).

Overall, 38 exotic invertebrates found at ES have the potential to be transported with oysters (Table 1) and may have been introduced to ES by this mechanism, although many are also associated with other transport mechanisms. (Ironically, this list does not include any of the four oyster species themselves; oysters never became established at ES, while many species unintentionally transported with them did.) While about two-thirds of exotic species found in ES are potentially associated with oysters, only about half of those found only in SFB are (Table 3A). This significant difference suggests that oyster culturing was relatively more important as a mechanism of introduction for ES than SFB.

Two examples illustrate the role of oyster-associated introductions at ES. The Japanese mud snail (*Batillaria attramentaria*) was likely introduced with Asian oysters in the 1920s or 1930s; it was detected in a shipment of Asian oyster spat sent to ES in 1929 (Bonnot, 1935b). This species is now easily the most abundant macroscopic animal species at ES (Fig. 4a). Based on densities measured by Byers (1999), we estimate that upwards of 10^9 Japanese mud snails are living in ES! This exotic can outcompete a similiar native snail, *Cerithidea californica*, due to more efficient conversion of resources into growth, lighter parasite loads, higher dispersal rates, and better tolerance of hypoxia (Byers, 2000a–c). The Japanese mud snail, found on this coast only at estuaries with a history of oyster culturing, is gradually displacing the native species in areas where they co-occur (Byers, 1999).

A second example is the sponge *Hymeniacidon ?sinapium*, one of the most conspicuous creatures in upper ES (Fig. 4b), which forms massive, bright orange balls with frilly protrusions. In addition to occurring on or near hard substrate such as gravel bars or drainage pipes, healthy individuals are found unattached on mud, an unusual habitat for sponges. This species was described by de Laubenfels (1930), who found it to be

Table 3
Comparison of potential transport mechanisms of exotic species for Elkhorn Slough and San Francisco Bay[a]

Invaders in	Yes	No	Total
(A) Oyster culture a potential transport mechanism			
Invaders in			
Elkhorn Slough	38 (68)	18 (32)	56
San Francisco Bay	63 (49)	66 (51)	129
(B) Oyster culture or ship fouling a potential transport mechanism			
Invaders in			
Elkhorn Slough	53 (95)	3 (5)	56
San Francisco Bay	103 (80)	26 (20)	129

[a] (A) Exotics associated with oyster culture. Yes, oyster culture is included as a possible transport mechanism for species in Table 1; No, it is not. (B) Exotics associated with either oyster culturing or ship fouling. Yes, oyster culture *or* ship fouling are listed as possible transport mechanism for species in Table 1; No, neither oyster culture or ship fouling listed as a possible transport mechanism. Number of exotic species is followed by percentage, in parentheses. A chi-square test revealed that patterns differed significantly between the two groups for both comparisons; for (A) $P=0.02$, $\chi^2=5.70$; for (B) $P=0.01$, $\chi^2=6.47$.

very abundant in beds of Atlantic oysters in Newport Bay and other southern Californian bays (de Laubenfels, 1932); we therefore postulate the species was introduced to ES with oysters. (*H. sinapium* is probably a junior synonym of *Hymeniacidon caruncula* or another Atlantic species; the genus comprises a number of very similar, likely synonymous species, and is in need of taxonomic revision.) The abundant orange sponge at ES may be influencing community composition, by its vigorous filtering activities, and by providing firm substrate in soft-bottom habitats.

4.2.2. Fouling on boats and ships

Besides oyster culturing, the other major mechanism likely to be responsible for introducing exotic species to ES is ship fouling. Most exotic species in ES (70%) are associated with ship fouling (Table 1), and therefore, could readily have been transported to ES on boats that picked up fouling species on their hulls while anchored in areas with abundant established populations of invaders. Boat traffic between Moss Landing (at the mouth of ES) and other regional harbors has a long history, and frequent voyages between Moss Landing and San Francisco have been documented at least as far back as the mid-1800s (Silberstein and Campbell, 1989). Today, boat traffic between Moss Landing and other local ports continues to be common (S. Schieblauer, Monterey Harbormaster, personal communication; J. Stilwell, Moss Landing Harbormaster, personal communication). The 600 or so resident fishing and pleasure boats mostly travel short distances up and down the coast. For instance, many fishing boats from the Monterey Bay region travel annually to the SFB area to catch herring, and when fishing is poor or weather bad, often remain there for long periods before returning to Moss Landing. There is also an annual migration of fishing boats along the coast, bringing a temporary influx of boats to Monterey Bay from other regional harbors as far south as Baja California, Mexico, and from as far north as Alaska (S. Schieblauer, personal communication). In contrast to the lively regional boat traffic, very few if any boats arrive at Moss Landing Harbor directly from distant seas.

The burrowing isopod *Sphaeroma quoyanum* illustrates the role of ship fouling at ES. Originally from Australia and New Zealand, *S. quoyanum* was first reported in SFB in 1893. It rapidly spread throughout California bays and harbors, almost certainly via ship fouling (Cohen and Carlton, 1995). The burrows of this isopod riddle virtually every bank we examined at ES, perhaps exacerbating already high rates of tidal erosion (S. Stout Bane, in preparation). Accompanying this invader at ES, as at SFB (Cohen and Carlton, 1995), is a tiny commensal isopod, *Iais californica*, which clings to *Sphaeroma*'s ventral surface. The role of commensals such as this species, of parasites (such as the trematode *Cercaria batillariae* that accompanied the Japanese mud snail to ES), and of mutualists in shaping estuarine invasion success is mostly unexplored.

4.2.3. Other mechanisms of introduction

Oyster culturing and ship fouling can account for almost all introductions to ES; of the 56 exotic species found ES and SFB, only three (5%) are not associated with either ship fouling or oysters (Table 3B). In contrast, significantly more (20%) of the exotic species found only in SFB are associated exclusively with other transport mechanisms (Table 3B). In particular, ballast water dumping is considered to be responsible for the majority of recent introductions to SFB (Cohen and Carlton, 1995) and to other large estuaries around the world (Carlton, 1985; Ruiz et al., 1997). Large international vessels with extensive ballast tanks very rarely dock at Moss Landing Harbor (J. Stilwell, personal communication), or even enter the Monterey Bay area (S. Shieblauer, personal communication), so ballast water discharge is not an important mechanism of introduction to ES.

Besides oyster culturing and boat traffic, a variety of other mechanisms could potentially introduce exotic species to ES. These include intentional introductions for fisheries, aquaculture, or biocontrol efforts, and unintentional transport with seaweed used to pack bait or seafood. For instance, the soft-shell clam *Mya arenaria* is known to have been planted in Santa Cruz and Tomales Bay (Hanna, 1939) and might also have been intentionally introduced to ES. Another such example comes from the planting of native eelgrass (*Zostera marina*) from various West Coast embayments (e.g. Coos, Humboldt, Tomales Bays) in ES in 1990; plants were transplanted in a matrix of surrounding sediment that could have included some of the exotic species established in these places. Such introductions are probably rare events and have been found to account for only a small percentage of invaders in SFB (Cohen and Carlton, 1995). We suspect that due to lower human activity levels at ES, these types of introductions are even less common there.

4.3. The importance of intraregional transport

4.3.1. Spread between vs. within regions

The initial invasion of a new region by an exotic species occurs, by definition, by *inter*regional mechanisms. Worldwide, international vessels and cultured oysters arriving directly from distant waters are the most common culprits, inadvertently transporting exotic species between regions (Carlton, 1985; Ruiz et al., 1997). The movement of vast volumes of water in ballast tanks of international vessels has been singled out as the most important current source of new estuarine invasions (National Research Council, 1996). Focus on such interregional mechanisms responsible for invasions has understandably resulted from investigations of large estuaries such as SFB, where international shipping (fouling on hulls and ballast water) is considered responsible for most recent introductions (Cohen and Carlton, 1995).

After an exotic species initially invades a new bioregion and becomes established, it may spread within the region by *intra*regional mechanisms including boat traffic, exchange of oyster stock by growers in different bays, and natural dispersal of larvae on currents (Zevina and Kuznetsova, 1965; Bell et al., 1987; Geller, 1994). Such routes of transport are likely to be very important for invasions of ES and other small estuaries. The 18 exotic species not associated with oyster-culture (Table 3a), the only significant interregional transport mechanism for ES, must have arrived via intraregional spread. Indeed, many of the remaining 38 ES species that are associated with oysters may have been transported intraregionally as well, since oysters were transferred between bays, and since most of these species are also associated with other intraregional mechanisms such as ship-fouling (Table 1). Furthermore, intraregional spread must account for the new invasions of ES that have apparently continued unabated (Fig. 3) in the decades following the decline and cessation of oyster culturing. Intraregional transport mechanisms have received little attention in the published literature, and yet our results suggest that they are critical to a full understanding of the phenomenon of estuarine invasions.

4.3.2. International ports as stepping stones for invaders

Due to their heavy exposure to *inter*regional transport mechanisms, large estuaries with international shipping become sources for *intra*regional spread. SFB, with its rich exotic fauna, likely plays an especially important role as a source of exotic species arriving at ES. Invaders at ES appear to be a nested subset of SFB exotic species: 51 of the 56 exotic ES species are found in SFB. A χ^2 contingency analysis showed that these 51 species are not a random subset of the 129 marine invertebrate invaders found in SFB, but instead disproportionately represent those species with access to intraregional transport mechanisms. Only 3/51 (6%) of SFB species shared with ES were not associated with ship-fouling or oyster culture. In contrast, a far greater proportion (23/78 = 29%) of species limited to SFB was not associated with these two mechanisms. This highly significant ($P = 0.001$, $\chi^2 = 10.68$) difference suggests that SFB exotics with access to intraregional transport are the source of many invasions of ES.

Three examples of recent invasions of ES illustrate how SFB can act as a stepping stone for exotic species. The Australian reef-forming tubeworm (*Ficopomatus enigmaticus*), the European green crab (*Carcinus maenas*), and the western Pacific tortellini snail (*Philine auriformis*) all invaded SFB by interregional transport before spreading along the coast. The tubeworm likely arrived at SFB fouling an international ship. Reefs of this worm were first noted in SFB in 1920 (Cohen and Carlton, 1995). Over 70 years later, it was first reported at ES, by a student (J. Alicea) in an unpublished class report (Moss Landing Marine Laboratories, Marine Ecology, 1994). Alicea found extensive reefs only in one area in the lower Slough system (site 1, Fig. 1); no reefs were found in the upper Slough (sites 9–10) despite thorough searches. Five years later, we found extensive reefs at site 10, and smaller patches at site 9. The tubeworm is known from nowhere else on this coast besides SFB and now ES; it seems to spread very slowly by intraregional transport, likely via fouling on regional boats. Once the worm is introduced and established, however, it can become locally dominant. Vast reefs now cover hard substrate in parts of ES (Fig. 4c), and the distribution of the worm in this estuary is probably still expanding.

The European green crab (Fig. 4d) has only recently become established in western North America. Juvenile green crabs are found among the algae used as packing material for bait and seafood sent from the Atlantic coast, where the species is abundant, so this route of transport seems mostly likely for its introduction (Cohen and Carlton, 1995). First noted in SFB in about 1989 (Cohen et al., 1995), the crab has undergone a remarkably rapid range expansion to the north and south (Grosholz and Ruiz, 1995). Green crab individuals have been reported from as far north as Vancouver, BC (A. Cohen, personal communication) and as far south as Morro Bay, CA (E. Grosholz, personal communication). At Bodega Harbor in northern California, this crab has been shown to greatly reduce populations of native bivalves and crustaceans (Grosholz and Ruiz, 1995; Grosholz et al. 2000), and it may pose a threat to commercially important species such as oysters, clams, and dungeness crab (*Cancer magister*) on the west coast. The green crab first appeared in ES in 1994 (Grosholz and Ruiz, 1995). Not known to be associated with boat traffic, green crabs probably spread to ES and elsewhere along the coast via natural larval transport on currents. A southward current runs along this region of coast from about March to July, such that a larva could be passively transported the 150 km from SFB to ES within a few weeks (Paduan and Rosenfeld, 1996); Grosholz (1996) calculated that larval transport could easily account for the rate of spread of the green crab along this coast.

Likewise, the tortellini snail probably spread to ES from SFB by transport of larvae on currents. Tortellini snails were first observed in SFB in 1992, most likely transported via ballast water, and were soon afterwards seen in Bodega Harbor, to the north (Gosliner, 1995). Voracious predators on bivalves, tortellini snails have the potential to profoundly impact benthic communities. By 1995, the tortellini snail was abundant in channels in ES (J. Engel, personal communication). All three of these examples illustrate that intraregional spread can occur by different mechanisms, and in separate events, than interregional transport.

4.3.3. *Preventing future intraregional invasions*

Invasive marine invertebrates are difficult, if not impossible, to eradicate once well-established and widespread. New colonizations can perhaps be removed to prevent establishment, but such efforts would require early detection of invasions. Unless the biota of estuaries such as ES is regularly monitored, such early detection is not possible. The other key management strategy is of course to focus on prevention. As a rule, the more propagules (adults, larvae, spores, or seeds) of an exotic species that arrive in an area, the more likely it is to become successfully established, given physical suitability of the new location (Williamson, 1996). We recommend two approaches to reduce the influx of invasive propagules to estuaries such as ES.

One management approach is to decrease regional source populations of invaders. Every new species that arrives and becomes established at SFB has the potential to subsequently spread. So policies limiting *inter*regional transport, such as ballast water treatment regulations, translate into fewer new *intra*regional invasions. The importance of limiting interregional mechanisms, particularly those associated with international shipping, has recently gained significant recognition (e.g. National Research Council, 1996), although the indirect benefits to estuaries without international shipping have not been emphasized.

A second management approach is to directly limit intraregional transport mechanisms. There is nothing that can be done to stop the natural diffusive spread of species, for instance by larvae travelling on currents. However, as our results show, anthropogenic transport is responsible for many transfers of exotic species between estuaries. Mechanisms for reducing transport due to all of the human-related mechanisms discussed above can be readily envisioned. Hulls of boats can be scrubbed after prolonged visits to major harbors, and contents of live wells could be discharged into treatment facilities. Bait and its algal packing material could be disposed of into garbage containers. Oysters and other aquaculture organisms could be thoroughly cleaned before being exchanged between bays. Such measures have received little attention, and would require substantial educational efforts, and perhaps regulatory policy, in order to be effectively implemented.

4.3.4. *Developing a predictive approach to intraregional invasions*

For predictions about new invasions and for control of existing ones, an understanding of the processes that underlie successful vs. failed invasions is essential. A better theoretical framework is needed for intraregional invasions. Based on our results, we suggest that two areas will be particularly fruitful. First, it is important to examine intraregional dispersal mechanisms to identify which species have access to transport mechanisms and are thus likely to become introduced to multiple estuaries. The significant difference we found in transport mechanisms for SFB species that did vs. did not invade ES suggests that dispersal opportunity is one good predictor of estuarine invasion. The 23 species found only in SFB that are not associated with oysters or ship fouling simply had less opportunity to invade ES. Second, we need a better understanding of the causes of local extinctions of populations of invaders following initial successful establishment. In ES, at least five conspicuous invasive species that were once established are now absent or at least so rare that they were not found in our fieldwork. Determining whether competition, predation, or parasitism by native species, say, or perhaps episodic challenging physical conditions led to the demise of these populations would provide valuable insights for controlling other invaders and for restoring native habitats in such a way as to minimize future invasions. The theory of island biogeography (MacArthur and Wilson, 1967), with its focus on local colonizations and extinctions, might serve to characterize the community dynamics of invasions within a region. Almost all of the exotic invertebrates reported from the northeastern Pacific coast are found in bays and estuaries, not along the open coast, so the metaphor is ecologically apt, with isolated "islands" of estuarine habitat along the coast. Comparisons of fauna among multiple embayments would allow more rigorous examination of the influence of major ports on nearby bays and estuaries. Important questions include the role of size (do large bays have more exotic species than small ones, and is this due to higher colonization rates, or lower extinction rates?) and distance (do nearby estuaries have a more similar exotic fauna than distant ones?). For understanding the population dynamics of single invaders, metapopulation models and their variants (Harrison, 1991) might be relevant for examining patterns of local extinction and re-colonization due to migration between estuaries. Future studies that test hypotheses based on such models will allow us to better predict the patterns and consequences of intraregional invasions.

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