

A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds

Susan L. Williams¹ and Jennifer E. Smith²

¹Section of Evolution and Ecology and Bodega Marine Laboratory, University of California, Davis, California 94923; email: slwilliams@ucdavis.edu

²National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, California 93106; email: jsmith@nceas.ucsb.edu

Annu. Rev. Ecol. Syst. 2007. 38:327–59

First published online as a Review in Advance on August 8, 2007

The *Annual Review of Ecology, Evolution, and Systematics* is online at <http://ecolsys.annualreviews.org>

This article's doi:
10.1146/annurev.ecolsys.38.091206.095543

Copyright © 2007 by Annual Reviews.
All rights reserved

1543-592X/07/1201-0327\$20.00

Key Words

impact, invasive, macroalgae, native range, nonindigenous, vector

Abstract

We reviewed over 407 global seaweed introduction events and have increased the total number of introduced seaweed species to 277. Using binomial tests we show that several algal families contain more successful invaders than would be expected by chance, highlighting groups that should be targeted for management. Hull-fouling and aquaculture are the most significant sources of seaweed invaders and should be carefully regulated. The ecological effects of introduced seaweeds have been studied in only 6% of the species, but these studies show mostly negative effects or changes to the native biota. Herbivores generally prefer native to introduced seaweeds, and are unlikely to control spread, as they can do in other habitats. Undisturbed marine communities can be at least initially resistant to most introduced seaweeds aside from the siphonous green species; however, disturbances and eutrophication can facilitate invasion. Major research gaps include community-level ecological studies and economic assessments.

Invasder: a species that colonizes a region outside its natural biogeographical distribution

Invasive: a condition whereby a species becomes excessively abundant usually causing ecological or economic harm

Introduced seaweed: a marine species in the Phyla Charophyta, Chlorophyta, Ochrophyta, or Rhodophyta introduced beyond its native range by human activities, and successfully established

“Considering our present knowledge it will be many years before we will be able to predict with any degree of certainty the effects an introduced species may have on an existing ecosystem.”

Phycologist L. Druehl in a letter to *Science* (Druehl 1973) predicting the establishment of *Sargassum muticum* in the eastern Atlantic after Japanese oysters were introduced from British Columbia to France.

INTRODUCTION AND SCOPE OF REVIEW

Seaweeds make a substantial contribution to marine primary production and provide habitat for nearshore benthic communities (Mann 1973). Over 200 seaweed species support an international economy in primarily phycocolloid (algins, agars, and carrageenans) and food products valued at over U.S. \$6.2 billion (Zemke-White & Ohno 1999). Seaweed production has more than doubled over the past two decades. Through human activities including aquaculture, seaweeds have been introduced to non-native locations around the world. Excellent reviews on seaweed introductions have been recently published (Inderjit et al. 2006, Ribera & Boudouresque 1995, Ribera Siguan 2003, Schaffelke et al. 2006, Trowbridge 2006) as have case histories on specific species (Chapman 1998, Mathieson et al. 2003, Meinesz 1999). Regional reviews and checklists help document the arrival of new invaders into specific locations (Boudouresque & Verlaque 2002a, Castilla et al. 2005, Maggs & Stegenga 1999, Orensanz et al. 2002, Ribera Siguan 2002). The Global Invasive Species Database (<http://www.issg.org/database>) of the International Union for the Conservation of Nature (IUCN) provides extensive data (native/introduced ranges, references) on introduced seaweeds.

Our objective was to update and integrate the known information on global seaweed introductions and their ecological effects. Specifically we quantitatively assessed (a) the taxonomic affinities of introduced seaweeds, (b) their morphological characteristics (functional groups), (c) the native and introduced ranges of seaweed invaders, (d) the vectors of introduction, and (e) the ecological effects of introduced seaweeds on native biota and vice versa. Details of the physiology, molecular evidence of biogeographic affinities, economic impacts, and management of introduced seaweeds were beyond the scope of this review.

CLASSIFICATION AND ANALYSIS

We define an introduced seaweed (or invader) as a species belonging to the Phyla Charophyta, Chlorophyta, Ochrophyta (formerly Phaeophyta) or Rhodophyta that has been introduced beyond its native range through human activities and has become successfully established in the new locale. Information on each unique introduction was compiled from published scientific literature, books, and Algaebase (Guiry & Guiry 2007) and is shown in **Supplemental Table 1** (follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org/>). Taxonomic information included basic classification using the nomenclature accepted by Algaebase (Guiry & Guiry 2007) on February 2, 2007. Functional group categories

were assigned to each species after Steneck & Dethier (1994) and included filamentous, crustose, corticated foliose, corticated macrophyte, leathery macrophyte, articulated calcareous, and siphonous (a unique category for the Bryopsidales, see Vroom & Smith 2001).

Vector of Introduction

The vector for each unique introduction was recorded as reported in the literature using the following designations (Ruiz et al. 2000): unreported (no clear indication of mechanism), aquarium introductions (release of aquarium organisms into the wild), aquaculture (the intentional introduction of algae for cultivation), shellfish farming (the introduction of algae growing on or associated with cultured shellfish), ballast (propagules transported within ballast water or attached to ballast rocks), hull fouling (species attached to oceanic vessels), fishing gear, research, and “lessespian” immigrants (species that migrated through the Suez Canal since 1869).

Native and Introduced Ranges

The native distributional range for each introduced seaweed was recorded as reported in Algaebase (Guiry & Guiry 2007). To assess global patterns, broad geographic regions were defined as follows: NE, NW, SE, SW, and central Atlantic and Pacific oceans; Caribbean; Australia and New Zealand; Mediterranean; Indian; Antarctic; Arctic; and the Black and Caspian Seas.

Each introduction to a new region was entered as a separate entry in **Supplemental Table 1** [e.g., *Caulerpa taxifolia* has been introduced to three regions: the Mediterranean, California (NE Pacific), and Australia]. However, species that have secondarily spread to states or countries within a region were only recorded once.

Analyses and Data Summary

We used the total number of unique seaweed introductions (where species may be counted more than once) for most of our analyses. However, for all questions related to the taxonomic affiliation of invaders, the total number of species was used.

Because taxonomy has been shown to be a useful predictor for identifying potential invaders (flowering plants, Daehler 1998; and birds, Lockwood 1999), we tested whether certain algal families contained more introduced species than would be expected by chance. We used the binomial distribution to generate an expected number of invaders per family for all groups containing invaders. The number of species (n) in each family was taken from Algaebase (Guiry & Guiry 2007). The expected proportion (p) of invaders was calculated by summing the total number of invaders and dividing by the total number of known marine algal species. The probability of obtaining a value equal to the observed (X) or more extreme than the observed (both higher and lower) was calculated using a two-tailed binomial test (Zar 1999) using

Crustose: an alga exhibiting a crust-like morphology that tightly adheres to the substratum and can be fleshy or calcified

Corticated: algal morphology consisting of multiple cell layers, most regularly an outer pigmented cortical layer and an inner unpigmented medullary layer

Macrophyte: a macroscopic alga (seaweed)

the following equation:

$$R = (n! / X!(n - X)!) p^x q^{n-x},$$

where n is family size, X is the number of observed invaders per group, p is the proportion of species expected to be invasive and $q = 1 - p$. Within each family the cumulative two-tailed R value was then considered significant if it was <0.05 and marginally significant if it was <0.1 (arbitrary adjustments for multiple tests were not performed).

Another database for ecological effects was compiled using data from studies published in primarily international scientific journals, excluding proceedings and reports owing to their uncertain peer review. We separated studies into observational (lacking statistical analysis, limited comparisons, models, calculations), mensurative, or experimental categories. Mensurative and experimental studies included a replicated statistical design; experimental studies involved manipulations of native organisms and/or the introduced seaweed. Response variables were sorted into abundance, diversity, community structure (relative abundances), community function (primary productivity, nitrogen fixation), individual performance (survival, growth, reproduction, size), and feeding response (preference of introduced seaweed relative to native as food source or foraging habitat). We accepted the peer-reviewed statistical results if the effect could be categorized as changed (community structure), negative (lower compared to preintroduction or to native biota), no effect, or enhanced (higher relative to preintroduction or native biota) at $\alpha = 0.05$. “Case” refers to a single-response variable in a single study.

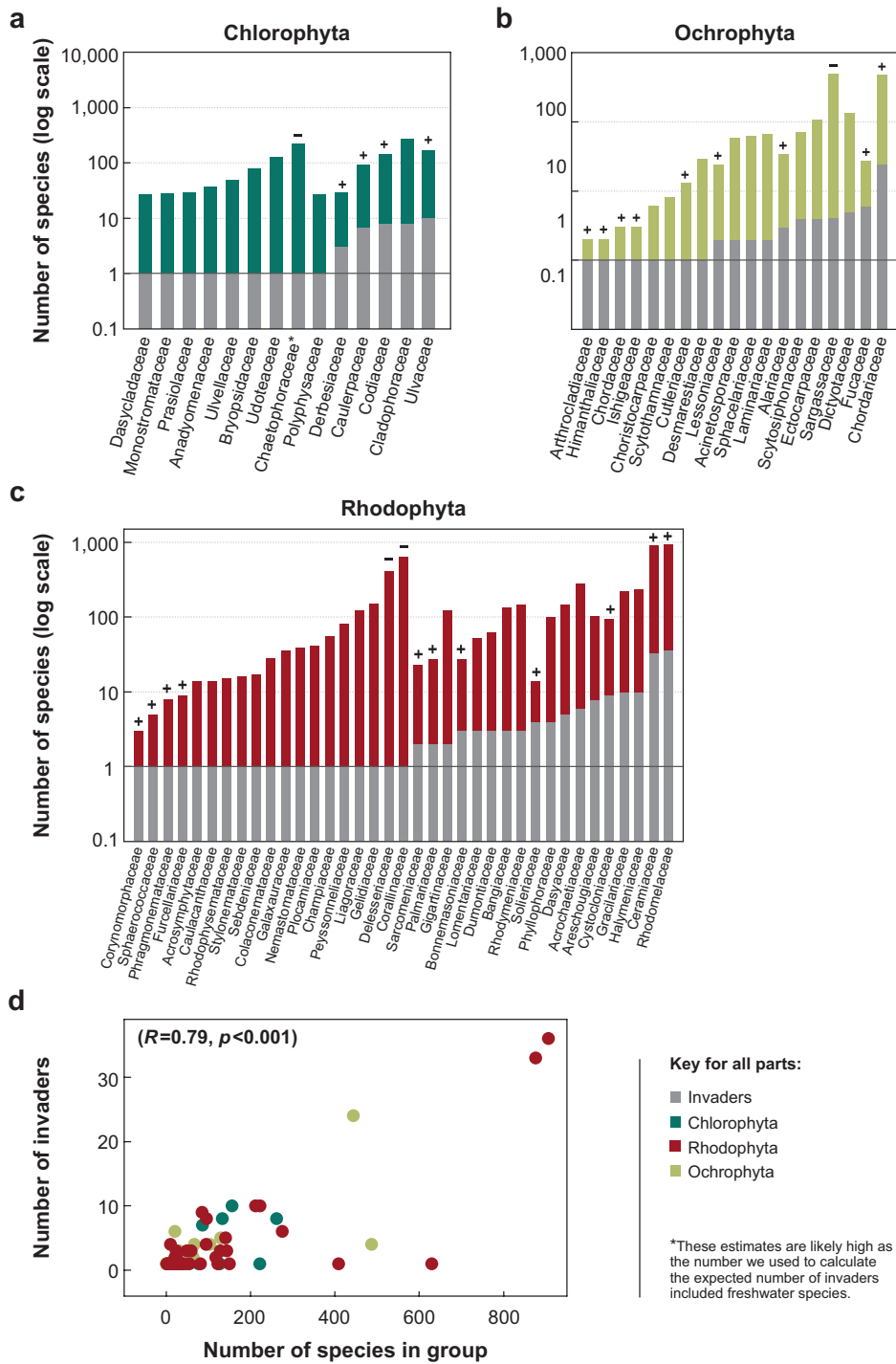
RESULTS

We estimate that the global number of introduced seaweed species is 277, increasing the previous estimates from recent reviews by at least 27 species (Ribera Siguan 2003, Schaffelke et al. 2006, Trowbridge 2006), with a total of 408 unique introductions (some species have been introduced to multiple regions) (see **Supplemental Table 1**).

The taxonomic distribution of introduced seaweeds includes 165 Rhodophytes (red algae), 66 Ochrophytes (brown algae), 45 Chlorophytes (green algae) and 1 Charophyte. Some groups, specifically larger families, have many more invaders than others (**Figure 1a–1c**), and in fact family size was positively correlated with invader number (**Figure 1d**). These results suggest that there may simply be proportional

Figure 1

The total number of species and the number of introduced species in a given family for (a) Chlorophytes, (b) Ochrophytes and (c) Rhodophytes. Bold + or – symbols designate families with significantly more ($p < 0.05$) or fewer introduced species than would be expected by chance, respectively, based on Binomial probability, whereas nonbold symbols show marginal significance at $p < 0.1$, respectively. (d) Pearson correlation between family size and invader number.



increases in invaders with family size, or perhaps greater evolutionary diversity and physiological strategies in these larger groups enhance invasion success.

Do Some Families Contain More Invaders Than Expected by Chance?

We formally tested whether the number of invaders in a given family was significantly higher or lower than expected by chance. The two green algal families Caulerpaceae and Codiaceae, which contain some of the most well-known introduced seaweed genera (*Caulerpa* and *Codium*), contain significantly more invaders than expected by chance (**Figure 1a**). The Derbesiaceae and Ulvaceae also contain more introduced species than expected by chance. Many species in the Ulvaceae are weedy and are known for their capacity to form nuisance blooms in response to nutrient pollution (Valiela et al. 1997). The green algal family Chaetophoraceae contains significantly fewer species than expected by chance because it is a large family with few invaders (and many freshwater species).

Of the brown algal families the Chordariaceae, Fucaceae, and Alariaceae (marginally significant) all contain more introduced species than expected by chance (**Figure 1b**). The Chordariaceae is a very diverse group containing over 444 species and 24 invaders, including the filamentous and often epiphytic genera *Punctaria*, *Sphaerotrichia*, and *Asperococcus*, and larger more fleshy genera such as *Leathesia* and *Hydroclathrus*. Among the Fucaceae algae, 6 of the 16 species in the genus *Fucus* have been successfully introduced, suggesting that this genus is highly invasive. The Alariaceae contains 31 species and 3 introduced species including the widely introduced and highly successful *Undaria pinnatifida*. Four other families also contain significantly more invaders than expected because they have fewer than 20 total species and at least one invader. Only the Sargassaceae, one of the largest brown algal families with 487 species, contains significantly fewer introduced species than would be expected by chance.

Among the Rhodophytes, many of the largest families contain significantly more introduced species than expected by chance (**Figure 1c**). Specifically, the Rhodomelaceae and the Ceramiaceae, with 906 and 876 species, respectively, each contain more than 30 introduced species. Most species in these groups are known for their ability to fragment, are uniaxial, and have relatively simple morphologies. The Gracilariaceae is marginally significant with 10 invaders (mainly aquaculture species) and 212 species. The Solieriaceae has a total of 10 species with 4 invaders. Among the Cystocloniaceae, 9 of 85 species have been successful invaders, but all belong to the genus *Hypnea*, suggesting that *Hypnea* may be an exceptionally invasive genus. Within the Areschougaceae, 8 of 96 total species have been successful invaders, including members of the genera *Kappaphycus*, *Eucheuma*, and *Sarconema*, many of which are intentionally introduced around the globe for commercial carrageenan production (Zemke-White & Smith 2006). Some other families have more invaders than would be expected by chance because they have a small number of known species and at least one invader (**Figure 1c**). Lastly, two red algal families had fewer introduced species than would be expected by chance. Interestingly, these include the rather diverse Corallinaceae (630 spp.) and the Delessariaceae (409 spp.), each with only one invader.

These taxonomic analyses highlight algal families with species that are more or less likely to be successful invaders based on current taxonomy and provide information useful for predicting future invasions. The groups that seem to have a great proclivity for invasion (green families Derbesiaceae, Codiaceae, Ulvaceae, and Caulerpaceae; the brown families Chordariaceae and Fucaceae; and the red families Rhodomelaceae, Ceramiaceae, Cystocloniaceae, and Areschougiaceae) should be carefully monitored.

Morphology and Functional Groups

Broad morphological and anatomical classifications may be useful to understanding if certain groups of algae tend to be more or less successful at invading new regions than others. Our analyses show that the majority of introduced seaweeds are either corticated macrophytes or are filamentous followed by corticated foliose, siphonous, and leathery macrophytes, and finally crustose algae (Figure 2a). The distribution and success of these different functional groups are likely to be the result of both the strength of the vector and the characteristics of the invaded habitat. We report the functional groups for only the large macroscopic phases of a given alga's life cycle, but many species of algae have a heteromorphic alternation of generations with spore- and gamete-producing generations having two distinct morphological entities for the same organism. Thus, for many brown algae in the Laminariales (such as *Undaria*), the sporophyte (a leathery macrophyte) is usually easy to detect, but the filamentous gametophyte is microscopic. Heteromorphic species may easily go undetected until reproduction has occurred and the larger macroscopic phase grows up.

Habitats with low physical disturbance and high productivity potential are expected to be dominated by corticated or leathery macrophytes (Steneck & Dethier

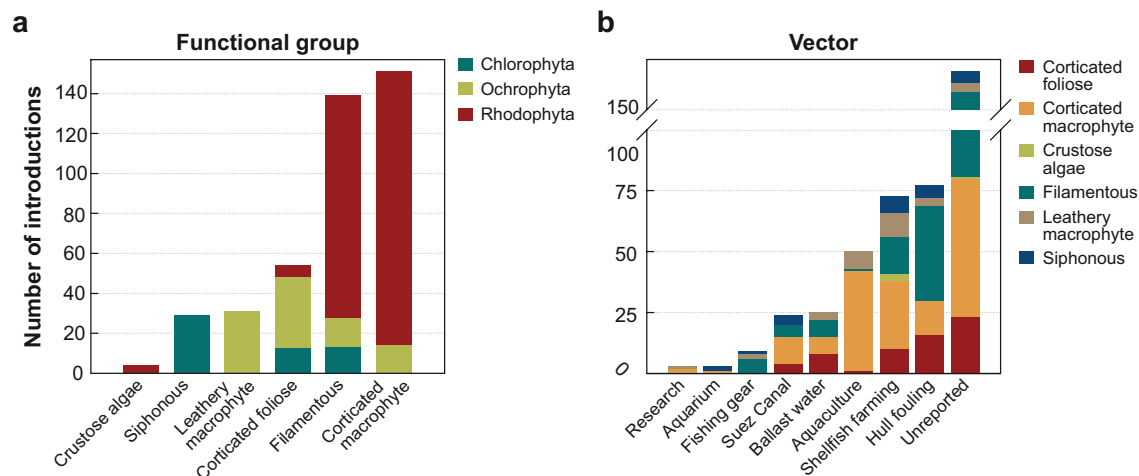


Figure 2

The number of seaweed introductions that (a) fall into different functional groups (Steneck & Dethier 1994) and Phyla and (b) are accounted for by different vectors or modes of introduction.

1994). This group includes genera such as *Gracilaria*, *Hypnea*, *Euclidean*, *Fucus*, and *Undaria* that have been introduced to shallow near-shore habitats around the world in association with aquaculture. Many of the genera in this group can also regenerate from vegetative propagules. Filamentous species are expected to be more successful in areas with higher disturbance potential, and here include many Rhodophytes (such as *Acanthophora*, *Polysiphonia*, and *Womersleyella*), Ochrophytes (such as *Ectocarpus* and *Stictyosiphon*), and Chlorophytes (including species of *Cladophora* and *Chaetomorpha*). Many of these filamentous species can readily fragment, are early colonizers, and can be found in a number of disturbed environments including harbors. Corticated foliose species are common in areas with moderate disturbance and productivity potential and include brown algae such as *Padina*, *Dictyota*, and *Colpomenia*, green algae such as *Ulva*, and fewer reds but include species of *Porphyra*. The large leathery macrophytes are expected to be most successful in areas with high productivity potential, as these species support proportionally more nonphotosynthetic tissue than the other functional groups (Littler et al. 1991). Thus, genera such as *Undaria*, *Sargassum*, and *Fucus* have largely been most successful in temperate, high-nutrient regions. The majority of the successfully introduced green algae are siphonous, can occupy a broad range of habitats, and belong to the order Bryopsidales. Some of the common invaders include species from the genera *Codium*, *Caulerpa*, and *Bryopsis*. These siphonous algae are all unicellular and are composed of either simple multinucleate tubes (e.g., *Bryopsis*) or form elaborate morphological configurations from a complex network of interconnected tubes with millions of nuclei (e.g., *Caulerpa*). The siphonous construction of these algae can allow for rapid growth, wound healing and fragment generation, and propagation (Wright & Davis 2006)—characteristics that have likely influenced the invasion success of many of these species, most notably *Caulerpa* spp. (Smith & Walters 1999). Lastly, crustose algae are expected to dominate in areas with high physical disturbance and low productivity potential, that is, environments that are not likely to receive many anthropogenic introductions. Further, only a single crustose alga, *Lithophyllum yessoense*, has been reportedly introduced to the Mediterranean and the NE Atlantic. Interestingly, not a single species in the diverse articulated calcareous functional group (including the genera *Halimeda* and *Corallina*) has been introduced. Perhaps these calcified species have very restrictive physiological tolerances, or they may simply lack appropriate propagules to disperse via anthropogenic activities. In summary, a combination of both the characteristics of the recipient environment and the type of vector can be useful in predicting the type of algal functional group that will likely be successful.

Vectors and Modes of Introduction

Information regarding the mechanism of introduction was lacking for 40% of the known algal introductions, yet there seemed to be strong evidence that these species were indeed introduced (e.g., discontinuous distribution in relation to the native range). Interestingly, almost half of these cases were filamentous algae, which are difficult to identify without microscopy and thus can go undetected until thorough surveys are completed. Of the reported modes of introduction, hull fouling

(77 introductions) and shellfish farming (73 introductions) are nearly equivalent in terms of the number of successful introductions (**Figure 2b**). More than 50% of the species introduced via hull fouling are filamentous, suggesting that this functional group along with some of the weedy corticated foliose genera such as *Ulva* can withstand transport in fouling communities.

Red corticated macrophytes are commonly introduced in association with shellfish farming. Many of the other species introduced via shellfish aquaculture come from a diverse array of functional groups, as any species that can colonize the shells of the commercial species can “hitchhike” into new environments (Naylor et al. 2001). Additionally, species used as packing material for fish or shellfish can easily be transported to new regions, as has occurred with species of *Fucus* in Europe and *Ascophyllum* on the west coast of North America.

The seaweed species that are most commonly cultivated around the world, either for colloid production (carrageenan and agar) or for food, are corticated or leathery macrophytes. The success of cultivated species in the new region is not surprising because many have been selected specifically for their robustness, tolerance to a wide range of physical conditions, propensity for rapid growth, and ability to propagate vegetatively (Naylor et al. 2001).

Although ballast introductions are generally common for marine species (Carlton & Geller 1993), especially invertebrates, they account for only 10% of reported seaweed introductions. Of these most are split among red and brown corticated or foliose macrophytes, leathery macrophytes, and filamentous species. Surprisingly very few species of green algae account for reported ballast introductions, despite their motile microscopic spores and gametes. Ballast is a very diverse means of transportation for many different types of species because propagules can travel variously within the water as vegetative or sexual propagules or, more historically, settled on ballast rock. The absence of light for photosynthesis during transport might diminish their viability and help explain the low proportion of successful seaweed invasions that have occurred through ballast release.

The opening of the Suez Canal in 1869 has been responsible for less than 10% of documented seaweed introductions. These Lessepsian immigrants include 24 algal taxa distributed across several functional groups.

Fishing gear has accounted for just over 3% of reported seaweed introductions and includes mainly filamentous species as well as some corticated macrophytes and siphonous species. This vector is likely to be the more important for secondary introduction or spread once a species has become established in a given region as many fishing vessels do not cross broad oceanographic regions; however, derelict nets may.

The rapidly expanding aquarium industry only accounts for 1% of the total number of known introductions but is responsible for the most well-publicized and well-documented seaweed invasion, that of *Caulerpa taxifolia* in the Mediterranean (Meinesz 1999). Although public or commercial aquaria can easily prevent species introductions by taking the proper precautions, individuals with home aquaria may dump non-native organisms into the environment. However, proper education and outreach along with new legislation banning the possession of highly threatening

species (such as *Caulerpa*) can help to prevent this type of introduction (Padilla & Williams 2004, Stam et al. 2006, Walters et al. 2006).

The more general categories of shipping (hull fouling plus ballast) and aquaculture (direct cultivation of seaweeds and the indirect introduction via shellfish aquaculture) compose over 85% of known vectors for documented introductions (with 102 and 121 introductions, respectively). These results closely parallel those found by Ribera Siguan (2003) despite the near doubling of species included in the present analysis.

Native and Introduced Species Distributions

The Mediterranean is the most heavily invaded region in the world for introduced seaweeds, with over 132 invasion events accounting for more than 33% of the total number of invasions (Figure 3a). This region has been extensively studied, having many phycologists and many studies to catalogue introduced species (Boudouresque et al. 1994, Boudouresque & Verlaque 2002b, Occhipinti Ambrogi 2000, Ribera

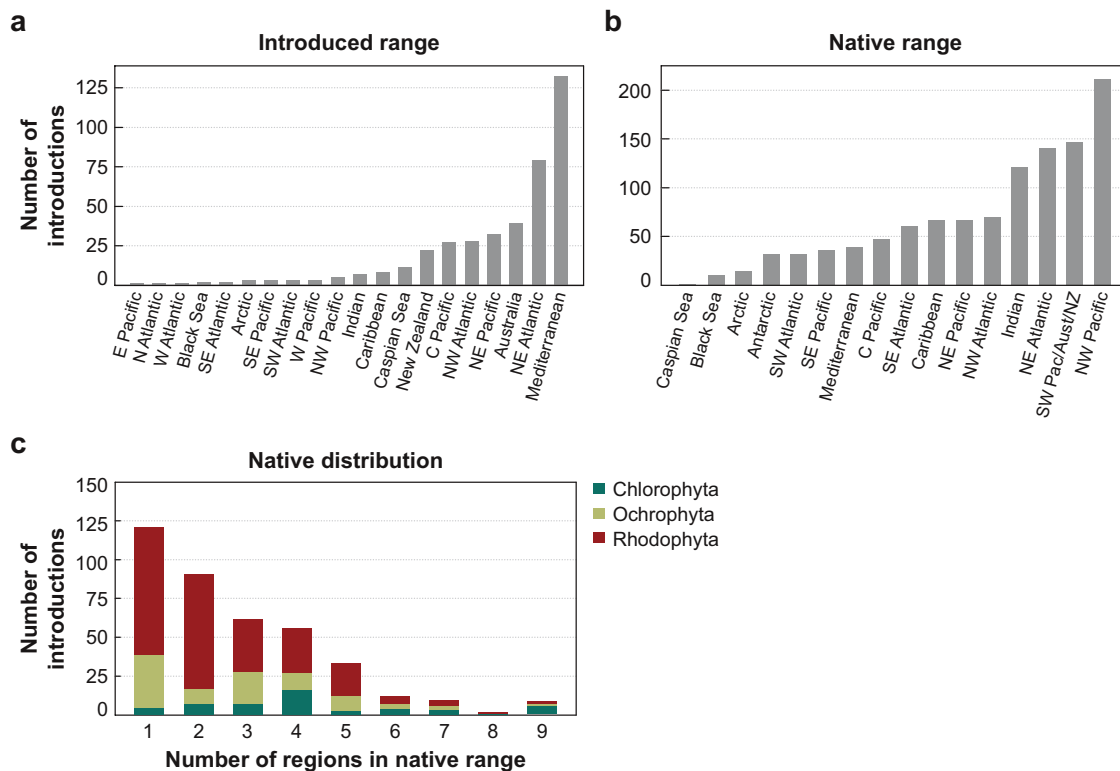


Figure 3

The (a) introduced range and (b) native range of all seaweed introductions, and (c) the number of regions in which each seaweed invader is native.

Siguan 2002). The NE Atlantic, including the North Sea, the Baltic Sea, and the eastern Atlantic Islands, has had 79 seaweed invasions accounting for just under 20% of the total. This region is also rich with historical data and species inventories, making detection of introduced species probable. Australia has documented 39 introductions accounting for approximately 10% of the global total. New Zealand, the NE Pacific, the NW Atlantic, and the central Pacific have all had somewhere between 20–32 invasion events making up between 5% and 8% of the total number of invasions. Many other regions have documented between 1–11 invasion events each, accounting for less than 5% of the total. Interestingly there is very little information available on introduced seaweeds from the tropics (Coles & Eldredge 2002). The above patterns are likely related to a number of factors including the history of research and phylogenetic expertise in a given region and, hence, the ability to detect an invader and the frequency and intensity of inoculation events.

We were unable to conduct an assessment of the specific source regions for all introduced species and were instead interested in determining if there was overlap in the native ranges of invaders. These results suggest that the majority of successfully introduced seaweed species are native to the NW and Indo-Pacific, an area containing the highest levels of biodiversity for a number of different taxa, including algae (Kerswell 2006); this is followed closely by Australia and New Zealand (**Figure 3b**). Species native to the European Atlantic coast are also successful invaders, as are species from the Indian Ocean, many of which were Lessepsian immigrants.

Finally, we hypothesized that the more broadly distributed or cosmopolitan species would be more likely to succeed in new regions than more narrowly distributed species. Contrary to this expectation, species native to only a single region make up a larger proportion of invaders than species with larger native ranges (**Figure 3c**). Clearly, species having narrow distributional ranges will be more easily detected in a new locale owing to discontinuous distributions. Furthermore, many species currently known to have cosmopolitan distributions may have in fact been early introductions prior to exhaustive taxonomic assessments. However, based on these analyses it seems that species that are native to only one oceanic region (and based on the previous section, the NW/Indo-Pacific) are more likely to be identified as successful invaders than species with more wide-ranging distributions.

Evidence for Ecological Effects

In the first systematic summary of the evidence for ecological effects of introduced seaweeds on native communities, we located 68 scientific journal articles with relevant information (11 observational studies, 27 mensurative, 28 experimental, and 2 combined from over 900 sources reviewed). Effects on native seaweeds and epiphytes were most common (**Figure 4**). Several different response variable categories were measured but changes in the abundance of native biota were most commonly reported (40% of 173 unique cases) (**Figure 4**; see also **Table 1**). The majority of the mensurative and experimental studies of introduced seaweeds showed negative effects (48%, 76 cases), particularly on native seaweeds. An additional 8% (13 cases) represented significant changes in community structure, whereas there was no detectable effect

Epiphyte: a plant or animal species that lives on (attached to) a typically larger plant

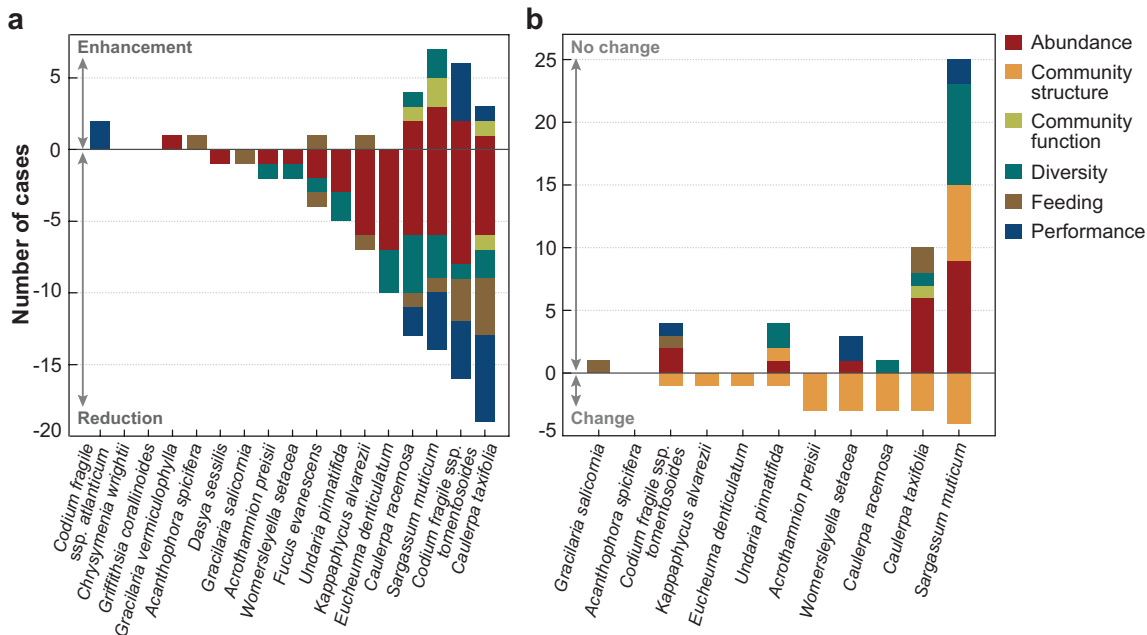


Figure 4

The number of cases (single-response variable in single study) that have documented (a) positive or negative effects and (b) change or no significant change to native species or communities at $\alpha = 5\%$.

reported for 30% (48 cases, mostly epiphytes), and an enhancement was found for 15% (23 cases).

The ecological effects of only 17 out of 277 introduced seaweeds have been studied, including *Caulerpa taxifolia* and *Undaria pinnatifida*, the only seaweeds listed among the world's 100 most invasive species (Lowe et al. 2004). *Sargassum muticum* and *C. taxifolia* were studied the most, whereas *U. pinnatifida* and red seaweeds were studied the least. No exclusively negative results were reported for any species; effects varied across studies, sites (Buschbaum et al. 2006, Wikström et al. 2006), and response variables. Only two species were reported as having no detectable negative effect [but see economic impact of *Gracilaria vermiculophylla* (Freshwater et al. 2006)]. Surprisingly, the ecological effects of numerous introductions of *Grateloupia turuturu* have not been studied.

Herbivores and introduced seaweeds. Compared to studies of effects on seaweeds and epiphytes, far fewer studies were devoted to effects on animals, primarily herbivores. Interactions between introduced seaweeds and native herbivores could alter trophic dynamics and seaweed spread if herbivores avoid eating the invaders ["enemy release" hypothesis (Keane & Crawley 2002)]. In the majority of feeding experiments, although introduced seaweeds were not preferred by generalist herbivores (littorines,

Table 1 Ecological effects of introduced seaweeds reported in observational, mensurative, and experimental studies

Introduced seaweed(s)	Effect ^a	Response variable ^b	Location (citation)
Observational			
<i>Caulerpa racemosa</i>	–	Introduced seaweed cover	Mediterranean (Piazzi et al. 2003a)
<i>Caulerpa taxifolia</i>	–	Seagrass biomass	NW Pacific (Williams & Grosholz 2002)
	–	Sea urchin feeding, behavior, spines, gonads	Mediterranean (Boudouresque et al. 1996)
	+	Nitrogen fixation	Mediterranean (Chisholm & Moulin 2003)
	–	Seaweed photosynthesis	Mediterranean (Ferrer et al. 1997)
<i>Codium fragile</i> ssp. <i>tomentosoides</i> and ssp. <i>atlanticum</i>	0	Seaweed density	NE Atlantic (Trowbridge 2001)
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	–	Kelp canopy cover	NW Atlantic (Mathieson et al. 2003)
	–	Seagrass survival	NW Atlantic (Garbary et al. 2004)
<i>Sargassum muticum</i>	+	Primary production, decomposition	NE Atlantic (Pedersen et al. 2005)
<i>Acanthophora spicifera</i> , <i>Gracilaria salicornia</i> , <i>Kappaphycus alvarezii</i>	–, +, 0	Herbivorous fishes feeding choice	Central Pacific (Stimson et al. 2001)
<i>Dasya sessilis</i> , <i>Chrysiomenia wrightii</i> , <i>Griffithsia corallinoides</i>	Δ	Seaweed distribution	Mediterranean (Vincent et al. 2006)
Mensurative			
<i>Caulerpa racemosa</i>	+	Polychaete species richness, abundance; macrofaunal species richness, abundance	Mediterranean (Argyrou et al. 1999)
	–	Seaweed richness, diversity, cover	Mediterranean (Piazzi et al. 2001)
	0	Seagrass leaf longevity	Mediterranean (Dumay et al. 2002a)
	+	Epiphyte biomass; seagrass primary productivity ^c	Mediterranean (Piazzi et al. 2003a)
	–	Seaweed species richness, cover	Mediterranean (Piazzi et al. 2003a)
	–	Encrusting and erect algae cover; total algal cover	Mediterranean (Balata et al. 2004)
<i>Caulerpa taxifolia</i>	–	Seaweed species richness, cover	Mediterranean (Piazzi et al. 2003a)

(Continued)

Table 1 (Continued)

Introduced seaweed(s)	Effect ^a	Response variable ^b	Location (citation)
	–	Encrusting and erect algae cover; total algal cover	Mediterranean (Balata et al. 2004)
	+	Epiphyte biomass; seagrass primary production ^c	Mediterranean (Dumay et al. 2002a)
	–	Seagrass leaf longevity	
	0	Seagrass areal extent	Mediterranean (Jaubert et al. 1999, 2003)
	0	Fish group size, group number, individual size	Mediterranean (Levi & Francour 2004)
	–	Fish foraging	
	–	Fish foraging, large size class	Mediterranean (Longepierre et al. 2005)
	0	Fish group size	
	–, 0	Herbivore abundance	SW Pacific (Gollan & Wright 2006)
	–	Bivalve reproduction	SW Pacific (Gribben & Wright 2006b)
	–	Fish species richness	SW Pacific (York et al. 2006)
	0	Fish abundance	
	Δ	Fish community structure	
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	–	Epifauna diversity, density	NW Atlantic (Schmidt & Scheibling 2006)
	+	Epiflora density	
<i>Fucus evanescens</i>	–	Epiflora biomass	NE Atlantic (Schueller & Peters 1994)
	–	Epiphyte biomass, species richness	NE Atlantic (Wikström & Kautsky 2004)
<i>Sargassum muticum</i>	0	Epifauna abundance; gastropod abundance	NE Atlantic (Viejo 1999)
	Δ	Epifauna community structure	
	–	Isopod abundance, size; amphipod abundance	
	0	Seaweed species richness, diversity	North Sea (Stæhr et al. 2000)
	–	Leathery and coarse seaweed cover	
	0	Epiflora diversity	North Sea (Bjørke & Fredriksen 2003)
	0	Canopy seaweed biomass	North Sea (Wernberg et al. 2004)
	+	Epibiota biomass	
	–	Seaweed biomass	NE Atlantic (Sánchez & Fernández 2005)
	+	Epiflora biomass	
	Δ	Seaweed community structure	

Table 1 (Continued)

Introduced seaweed(s)	Effect ^a	Response variable ^b	Location (citation)
	–, +	Epibiota species richness	North Sea (Buschbaum et al. 2006)
	0, Δ	Epibiota community structure	
	Δ	Infauna community structure	NE Atlantic (Strong et al. 2006)
	–, 0	Infauna diversity, evenness, body length	
	+, 0	Infauna dominance, abundance	
	+	Seaweed species richness, ephemeral seaweed cover	North Sea (Thomsen et al. 2006b)
	0	Leathery, branched, and encrusting algal functional groups cover; herbivore abundance	
	–, 0	Herbivore richness, abundance	North Sea (Wikström et al. 2006)
<i>Undaria pinnatifida</i>	0	Canopy seaweed cover; seaweed species richness; faunal species richness; community structure	SW Pacific (Forrest & Taylor 2002)
<i>Acrothamnion preisii</i> , <i>Womersleyella setacea</i> , turf	Δ	Seaweed community structure	Mediterranean (Piazzi & Cinelli 2003)
<i>Acrothamnion preisii</i> , <i>Womersleyella setacea</i> , <i>Caulerpa racemosa</i>	Δ	Seaweed community structure	Mediterranean (Piazzi & Cinelli 2003)
<i>Acrothamnion preisii</i> , <i>Womersleyella setacea</i> , <i>Caulerpa racemosa</i> , <i>Caulerpa taxifolia</i>	Δ	Seaweed community structure	Mediterranean (Piazzi & Cinelli 2003)
<i>Eucheuma denticulatum</i> and <i>Kappaphycus alvarezii</i> farm	–	Seaweed cover; seagrass density, biomass, cover; macrofaunal abundance, biomass	Indian Ocean (Eklöf et al. 2005)
<i>Gracilaria vermiculophylla</i>	+	Filamentous algal species richness, biomass	NW Atlantic (Thomsen et al. 2006a)
15 species	0	Seaweed species richness	Mediterranean (Klein et al. 2005)
Experimental			
<i>Caulerpa racemosa</i>	–, +	Seagrass density	Mediterranean (Ceccherelli & Campo 2002)
	+	Seagrass sexual reproduction ^c	
	–	Sea slug food choice	Mediterranean (Gianguzza et al. 2002)
	–	Introduced seaweed (<i>Caulerpa taxifolia</i>) size, growth	Mediterranean (Piazzi & Ceccherelli 2002)
	–	Seaweed species richness, cover	Mediterranean (Piazzi & Ceccherelli 2006)

(Continued)

Table 1 (Continued)

Introduced seaweed(s)	Effect ^a	Response variable ^b	Location (citation)
<i>Caulerpa taxifolia</i>	–	Seagrass density	Mediterranean (Ceccherelli & Cinelli 1997)
	0	Seagrass density	Mediterranean (Ceccherelli & Sechi 2002)
	–	Sea slug food choice	Mediterranean (Gianguzza et al. 2002)
	0	Snail, sea hare, and fish food choice	SW Pacific (Davis et al. 2005)
	–	Herbivore food choice, habitat choice	SW Pacific (Gollan & Wright 2006)
	–, 0	Herbivore survivorship	
	+	Bivalve recruitment	SW Pacific (Gribben & Wright 2006a)
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	–, 0	Sea urchin grazing	NW Atlantic (Prince & Leblanc 1992)
	–	Sea urchin grazing, reproduction	NW Atlantic (Scheibling & Anthony 2001)
	0	Sea urchin growth	
	+	Sea slug metamorphosis, postlarval growth, development	NE Atlantic (Trowbridge & Todd 2001)
	0	Kelp growth; crab and lobster abundance	NW Atlantic (Levin et al. 2002)
	–	Kelp recruitment; seaweed cover; sea urchin and littorine snail grazing; predatory fish abundance	
	–	Littorine snail density, feeding, growth	NW Atlantic (Chavanich & Harris 2004)
	–	Sea urchin grazing; kelp survival	NW Atlantic (Sumi & Scheibling 2005)
	+	Mussel recruitment, survival, density, size	Adriatic (Bulleri et al. 2006)
–	Seaweed density, biomass	NW Atlantic (Scheibling & Gagnon 2006)	
<i>Fucus evanescens</i>	–	Isopod food choice	Baltic Sea (Schaffelke et al. 1995)
	–, +	Littorine snails food choice; isopod food choice	NE Atlantic, North Sea (Wikström et al. 2006)
<i>Sargassum muticum</i>	–	Kelp recruitment	NE Pacific (Ambrose & Nelson 1982)
	–	Seaweed cover	NE Pacific (DeWreede 1983)
	–	Seaweed abundance, growth; sea urchin feeding	NE Pacific (Britton-Simmons 2004)
	0	Seaweed cover, species richness, diversity, community structure, succession	NE Atlantic (Sánchez & Fernández 2005)

Table 1 (Continued)

Introduced seaweed(s)	Effect ^a	Response variable ^b	Location (citation)
<i>Undaria pinnatifida</i>	–	Seaweed richness, diversity	SW Atlantic (Casas et al. 2004)
	0	Seaweed cover	Tasman Sea (Valentine & Johnson 2005)
	Δ	Seaweed community structure	Tasman Sea (Valentine & Johnson 2003)
	–	Kelps; tunicate	NE Atlantic (Farrell & Fletcher 2006)
<i>Gracilaria salicornia</i>	–	Fish food choice	central Pacific (Smith et al. 2004)
<i>Womersleyella setacea</i>	–	Native seaweed cover	Mediterranean (Airoldi 1998, 2000)
	0	Algal crust cover, mortality, fertility	

^a Δ, change; 0, no detectable change or effect; –, negative effect on, or not preferred to, native biota; +, enhanced effect on, or preferred to, native biota. Multiple entries indicate different results at different sites or times or with different native species within a single study. All mensurative and experimental effects were tested statistically in the cited study and reported here at alpha = 5%.

^b Response of native biota unless indicated as “introduced.”

^c Enhancements considered evidence of stress, not facilitation.

isopods, polychaetes, sea urchins, fishes), they were eaten, including *Caulerpa taxifolia* with its unique deterrents (Dumay et al. 2002b). In a few cases introduced seaweeds were preferred over at least one, often unpalatable, native species [e.g., the kelp *Agarum* (Britton-Simmons 2004, Prince & Leblanc 1992)]. Thus, introduced seaweeds do not escape completely from novel herbivores.

Despite eating introduced seaweeds, native herbivores have not been documented to control invader spread (Britton-Simmons 2004, Chavanich & Harris 2004, Conklin & Smith 2005, Davis et al. 2005, Gollan & Wright 2006, Levin et al. 2002, Sumi & Scheibling 2005, Trowbridge 1995). Strikingly, even *Undaria pinnatifida* escapes herbivore control despite being highly edible (farmed for human consumption) and rapidly consumed by herbivores (Thornber et al. 2004). In the Tasman Sea, sea urchins cannot keep up with annual growth of *Undaria* and they actually facilitate its spread by consuming native perennial seaweeds and opening space for settlement (Edgar et al. 2004; Valentine & Johnson 2003, 2005). Similarly, herbivores also facilitate highly unpalatable *Asparagopsis armata* in the Mediterranean (Sala & Boudouresque 1997). These general patterns where herbivores cannot control the spread of introduced seaweeds contrast with a recent meta-analysis showing that native generalist herbivores, particularly large vertebrates, provide biotic resistance to plant invasions on land and in freshwater and saltwater marshes (Parker et al. 2006). These differences may be due to the fact that large vertebrate herbivores are not as common in seaweed-dominated habitats.

Strict specialist herbivores are often sought for biocontrol of invasive plants with minimal effects on native species, although with great caution (Secord 2003). However, ascoglossan mollusks (sea slugs) specializing on siphonous green seaweeds were rejected as biocontrols for introduced *Caulerpa* and *Codium* because they can shift their

host preference over a short period (Thibaut et al. 2001, Trowbridge & Todd 2001) and can actually enhance the spread of introduced seaweeds through fragmentation (Harris & Mathieson 1999, Züljevic et al. 2001).

The majority of the studies concerning introduced seaweeds and herbivores have been laboratory feeding preference tests or field inclosures/exlosures of herbivores. Although food choices are informative, they can change over time (Trowbridge 1995) as can seaweed allocation to chemical deterrents (Wikström et al. 2006). How herbivores interact with introduced seaweeds also depends on their relative distributions and abundances, their encounter rate, and on whether predators exert top-down control.

Effects on native marine communities. Community-level ecological interactions involving introduced seaweeds constitute a major research gap. Indirect effects between trophic levels, the mobility of consumers, and restrictions on replication present research challenges. Recent community-level field experiments revealed important indirect effects between trophic levels. Such effects are not evident in single-response variables but can be elucidated through techniques such as structural equation modeling (Britton-Simmons 2004). For example, *Sargassum muticum* had an indirect negative effect on sea urchins through shading native kelp, their preferred food. An indirect effect was also evident in the replacement of a native kelp forest with *Codium fragile* ssp. *tomentosoides* (Levin et al. 2002, Scheibling & Gagnon 2006). This transition was facilitated by another introduced species [“invasional meltdown” (Simberloff & Von Holle 1999); when introduced species facilitate each other’s abundance or negative effects, their impacts on native communities can compound], the bryozoan *Membranipora membranacea*, which severely fouls kelp to the point of decline, opening space for *Codium*. Additional effects of *Codium* on the community varied across consumer functional groups; however, trophic support for the dominant predatory fish was predicted to change because its prey are associated with understory kelps. Other studies of mobile animals and foraging behavior in introduced seaweed communities are too few to generalize but most have reported at least a qualitative change (**Table 1**). Major shifts in community structure can occur even if species richness and biodiversity remain unchanged (Sax et al. 2005), as has occurred where *Sargassum muticum* has invaded (Sánchez et al. 2005, Stæhr et al. 2000). In addition, resilience of native communities may be reduced after invasion by seaweeds (Piazzi & Ceccherelli 2006, Valentine & Johnson 2003).

Studies on the long-term effects of introduced seaweeds on ecosystem processes are sorely needed (primary and secondary production, nutrient cycling; **Table 1**). The hypothesis that introduced seaweeds increase primary productivity, which could lead to higher consumer abundance (Pedersen et al. 2005, Thomsen et al. 2006a, Viejo 1999, Wernberg et al. 2004), requires investigation in natural communities. Generally unpalatable themselves, introduced seaweeds can support high abundances of palatable epiphytes, but epiphyte populations can be notoriously ephemeral food sources for consumers. We found no studies that assessed introduced seaweeds as trophic support for detritivores. Finally, an understanding of how introduced seaweeds alter

the flow of matter and energy through ecosystems must be considered along with any effects on biodiversity.

The invasibility of marine communities and the role of disturbance. We searched for studies on introduced species that addressed two core questions in invasion biology: (a) what conditions or properties (e.g., biodiversity) confer native communities with resistance to introduced seaweeds, and (b) does disturbance increase invasion potential? Factors that influence the invasibility of marine communities, including spatial scale, demographic and functional attributes of resident species, and positive interactions, are just beginning to be revealed in marine studies, which often only involve native species (Arenas et al. 2006, Dunstan & Johnson 2004, France & Duffy 2006, Sax et al. 2005). Furthermore, most research indicates that disturbance tends to increase invasibility of marine communities (Byers 2002, Ruiz et al. 1999). We found only 18 studies on introduced seaweeds that were relevant to the above questions (**Table 2**).

Undisturbed algal communities (turfs, foliose species, large canopy-forming kelps) can resist seaweed invasions, but only rarely enough to limit their impacts and spread (Andrew & Viejo 1998). The preemptive competitors *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum*, *Undaria pinnatifida*, and *Wormersleyella setacea* are able to invade readily upon disturbance and then persist (**Table 2, Figure 5**). Initial resistance of native marine communities can be overcome by high invader growth rates (Airoldi 2000), during different life history stages (Britton-Simmons 2006, Sánchez & Fernández 2006, Scheibling & Gagnon 2006), and under varying ecological conditions (Bulleri & Airoldi 2005). Long-term studies are thus important to document any weakening in the biotic resistance of native communities (e.g., Harris & Jones 2005).

The siphonous green seaweeds (*Codium fragile* ssp. *tomentosoides*, *Caulerpa taxifolia*, *C. racemosa* var. *cylindracea*) are strong interference (direct) competitors of seaweeds (Piazzi et al. 2001) and seagrasses (Ceccherelli & Cinelli 1997, Ceccherelli et al. 2002, Garbary et al. 2004). Native seagrass resistance to introduced seaweeds is important because seagrasses are declining in many areas around the world (Orth et al. 2006). Of the seagrasses studied in the Mediterranean, only continuous or dense patches of *Posidonia oceanica*, one of the largest and longest-lived seagrass species, can effectively resist introduced *Caulerpa* spp. (Ceccherelli & Campo 2002, Ceccherelli & Cinelli 1999a, Ceccherelli et al. 2000).

Does nutrient enrichment facilitate introduced seaweeds? Nutrient enrichment is among the most significant threats to coastal marine ecosystems and often leads to deleterious algal blooms (Howarth et al. 2002). Introduced seaweeds can be numerous and abundant in areas subjected to nutrient pollution (Boudouresque & Verlaque 2002b, Chisholm et al. 1997, Occhipinti Ambrogi 2000, Schueller & Peters 1994), suggesting that nutrient enrichment may enhance invasion success (Chisholm & Moulin 2003, Chisholm et al. 1997, Fernex et al. 2001, Jaubert et al. 2003, Lapointe et al. 2005, but see Klein et al. 2005). However, vectors and other factors that covary with pollution (**Figure 3**; Sant et al. 1996) can confound causality.

Invasibility: the susceptibility of a native community to the establishment of an introduced species

Table 2 Response of introduced seaweeds to experimental removals of native biota and to nutrient enrichment

Introduced seaweed	Response variable	Effect ^a	Type of experiment	Location (citation)
<i>Caulerpa racemosa</i>	Growth	+	Seagrass (<i>Posidonia oceanica</i>) removal	Mediterranean (Ceccherelli et al. 2000)
<i>Caulerpa racemosa</i>	Recolonization	–	Algal turf removal	Mediterranean (Piazzi et al. 2003b)
<i>Caulerpa taxifolia</i>	Density	0	Seagrass (<i>Cymodocea nodosa</i>) removal	Mediterranean (Ceccherelli & Cinelli 1997)
<i>Caulerpa taxifolia</i>	Density	+	Nutrient enrichment	Mediterranean (Ceccherelli & Cinelli 1997)
<i>Caulerpa taxifolia</i>	Density	0	Seagrass (<i>Cymodocea nodosa</i>) removal	Mediterranean (Ceccherelli & Sechi 2002)
<i>Caulerpa taxifolia</i>	Density	0	Nutrient enrichment	Mediterranean (Ceccherelli & Sechi 2002)
	Density, biomass, survival	0		
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	Cover	+	Mussel removal, spring	Adriatic (Bulleri & Airoidi 2005)
		–	Mussel removal exposed, summer	
		+	Mussel removal sheltered, summer	
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	Cover, growth	+	Seaweed removal	NE Atlantic (Scheibling & Gagnon 2006)
<i>Fucus evanescens</i>	Germling growth, survival	0	Nutrient enrichment (laboratory)	North Sea (Steen & Rueness 2004)
<i>Sargassum muticum</i>	Recruitment	+	Seaweed canopy removal	NE Pacific (Deysher & Norton 1981)
<i>Sargassum muticum</i>	Recruitment	+	Seaweed removal	NE Atlantic (Andrew & Viejo 1998)
<i>Sargassum muticum</i>	Germling growth, survival	0	Nutrient enrichment (laboratory)	North Sea (Steen & Rueness 2004)
<i>Sargassum muticum</i>	Recruitment	0	Seaweed removal	NE Pacific (Britton-Simmons 2006)
		0	Understory seaweed removal	
		+	Crustose + turf seaweed removal	
	Survival	+	Canopy + understory seaweed removal	
<i>Sargassum muticum</i>	Cover, length, density, recruitment	+	Nutrient enrichment	NE Atlantic (Sánchez & Fernández 2006)

Table 2 (Continued)

Introduced seaweed	Response variable	Effect ^a	Type of experiment	Location (citation)
	Cover, length, density	0	Seaweed canopy removal	
	Recruitment	–	Seaweed canopy removal	
<i>Undaria pinnatifida</i>	Recruitment	+	Seaweed canopy removal	Tasman Sea (Valentine & Johnson 2003)
<i>Undaria pinnatifida</i>	Recruitment	+	Seaweed canopy removal	Tasman Sea (Edgar et al. 2004)
<i>Undaria pinnatifida</i>	Recruitment	+	Seaweed canopy mortality	Tasman Sea (Valentine & Johnson 2004)
<i>Undaria pinnatifida</i>	Recruitment	0	Seaweed canopy removal	NE Atlantic (Farrell & Fletcher 2006)
<i>Asparagopsis armata</i>	Biomass	–	Herbivore exclusion	Mediterranean (Sala & Boudouresque 1997)
<i>Womersleyella setacea</i>	Cover	+	Seaweed removal	Mediterranean (Airoldi 1998)
<i>Womersleyella setacea</i>	Cover	+	Algal crust removal	(Airoldi 2000)

^aEffect indicates how the introduced seaweed responded to the experimental manipulation (disturbance) of the native biota or to nutrient enrichment. +, suggests resistance of native biota to introduced seaweed or enhanced response to nutrient enrichment; 0, indicates no detectable effect; –, suggests facilitation by native biota. All effects were statistically tested in the cited study and reported here at alpha = 5%.

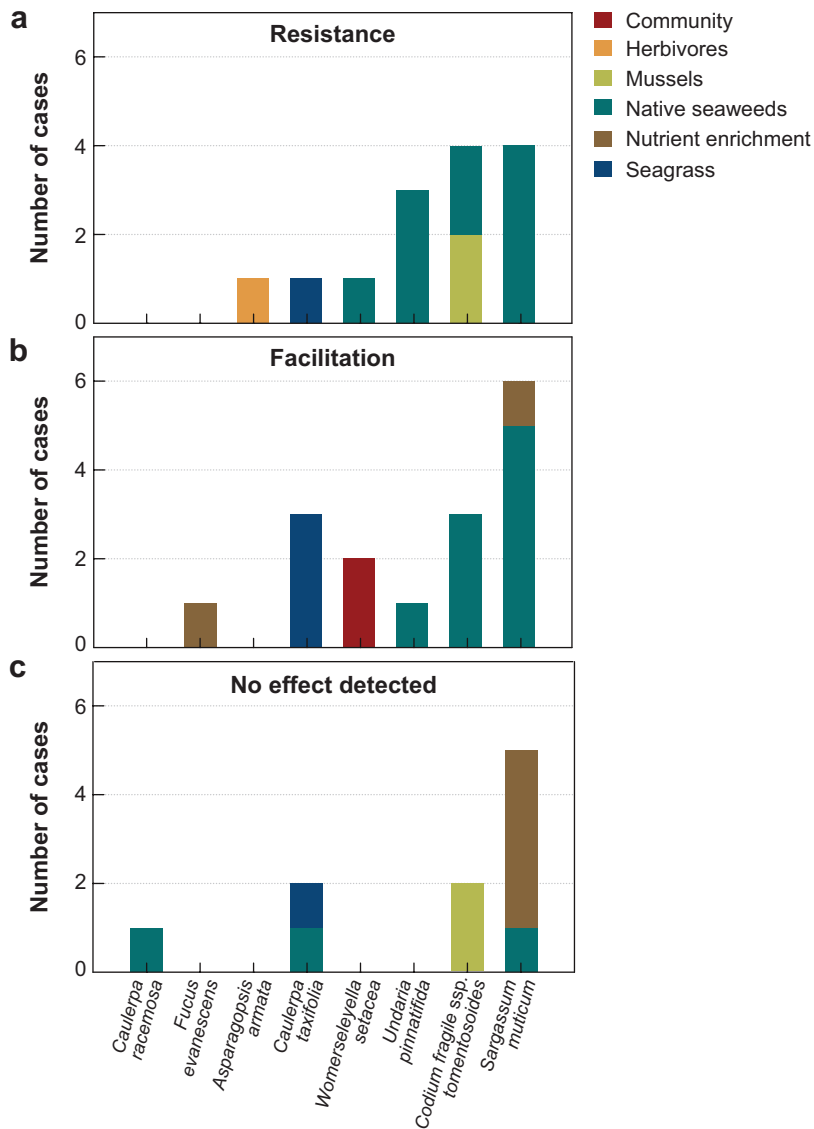
Direct testing of the nutrient enhancement hypothesis has been limited, and experimental results are mixed (Table 2). Sánchez & Fernández (2006) found that nutrient enrichment enhances *Sargassum muticum*. Because the native seaweed canopy offers little resistance to introduced *Sargassum*, eutrophication could promote its further spread. The most recent experimental studies have not supported the hypothesis that nutrient or organic enrichment enhances *Caulerpa taxifolia* (Ceccherelli & Sechi 2002, Terrados & Marbà 2006; see also Delgado et al. 1996), contrasting partially with earlier studies (Ceccherelli & Cinelli 1997, 1999b) and indirect evidence cited above.

WHEN INTRODUCED SEaweeds BECOME INVASIVE

Introduced species are considered to be invasive when they incur or are likely to incur negative ecological or economic impacts. Quantitative evidence from mensurative and experimental studies on just 6% of the seaweeds introduced to date shows that 13 of them are invasive by this definition and that native marine communities have little lasting resistance to these invaders, particularly if disturbed. This review provides a foundation for further analyses, risk assessment, and targeted management of introduced seaweeds. Of particular concern are the siphonous green seaweeds such as *Caulerpa* and *Codium*, which are well-known invaders, but also species of *Fucus* and *Hypnea*, which are less well known. In addition, the commercially cultivated red seaweeds (*Eucheuma denticulatum*, *Kappaphycus alvarezii*, *Gracilaria salicornia*, *Hypnea musciformis*) are also a concern because they are farmed next to coral reefs and over seagrasses in regions where labor is inexpensive. Reports of the economic and

Figure 5

The number of cases documenting that native communities (*a*) resisted, (*b*) facilitated, or (*c*) had no effect on an introduced seaweed.



social costs of these seaweeds are just coming to light (see Related Resources), but we predict they will have a major ecological impact in the future unless preventive steps are taken now, such as engaging phycologists and the industry to make the culture environmentally sustainable or to cultivate native species.

Existing recommendations for managing invasive species, including many seaweeds, in many affected countries and regions are too numerous to review here, but all share common elements: prevention as the most effective means to reduce future costs, early detection and rapid response when prevention fails, eradication

if possible, control as a last resort, public education and stakeholder engagement, and research in support of management (Lodge et al. 2006). As both shellfish and seaweed aquaculture and the aquarium trade are expanding rapidly, seaweed introductions will undoubtedly increase (Naylor et al. 2001, Padilla & Williams 2004), and it is likely that genetically engineered seaweeds will become available for culture (Walker et al. 2005). Evidence suggests that introduced seaweeds can have negative economic impacts and are incredibly difficult and costly to eradicate. Thus, we reinforce the recommendations that put forth repeatedly to sustain and increase efforts to prevent new introductions and control spread as quickly as possible (Lodge et al. 2006, Schaffelke et al. 2006).

SUMMARY POINTS

1. Some algal families contain significantly more introduced species than would be expected by chance, suggesting that these families are likely to be more invasive.
2. Siphonous green seaweeds, which include *Caulerpa taxifolia*, *C. racemosa*, *Codium fragile* spp. *tomentosoides* and spp. *atlanticum*, and several other *Caulerpa* spp., are highly successful invaders that compete directly with native species.
3. The Mediterranean and the NE Atlantic support the highest number of successful seaweed introductions.
4. Most of the introduced seaweed species in the world are native to the NW and Indo-Pacific. Species with narrower distributional ranges had higher numbers of introductions than the more cosmopolitan species, contrary to what has been predicted.
5. The most important vectors for seaweed introductions are fouling of vessel hulls and aquaculture (direct and indirect). Ballast water introductions are less common for seaweeds than documented for other marine species.
6. The ecological effects of only a limited number (6%) of introduced seaweeds have been tested; from these studies, the impacts tend to be diverse but are generally negative.
7. Native herbivores will consume introduced seaweeds, but they often prefer native species, they cannot control even edible introduced seaweeds, and in some cases they facilitate seaweed spread.
8. Native marine communities have little lasting biotic resistance to introduced seaweeds, particularly if a disturbance opens space for invasion.

FUTURE ISSUES

1. Management to prevent future seaweed introductions should focus on hull fouling, particularly by inconspicuous filamentous species and aquaculture

(both the direct introduction of algae and indirect introduction through shellfish farming) and species in the families with higher than expected probabilities of successful invasions because species in these families are among the most widespread and well-documented seaweed invaders in the world [including *Caulerpa* and *Codium* (the siphonous greens), *Fucus*, *Undaria*, *Asparagopsis* and *Hypnea*].

2. Manipulative community-level field studies in combination with modeling are needed to identify not only the impacts of introduced seaweeds on native communities but also the factors that influence invasibility for a more integrative understanding of invasive seaweed ecology.
3. Understanding the potential role of nutrient enrichment in facilitating seaweed introductions will require experiments that directly test the hypothesis and separate other factors that covary with increasing coastal eutrophication.
4. The economic costs of introduced seaweeds are emerging, and future assessments should include externalities [costs to society or native biota in addition to the identifiable direct costs associated with the specific economy (aquaculture products, eradication programs)].

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank James Carlton for valuable insight, Keith Hayes at CSIRO for contributing information on Australian species, the National Center for Ecological Analysis and Synthesis for logistics and support, Michael Guiry for assistance with taxonomy and for maintaining Algaebase, Stuart Sandin for help in programming, Daniel Simberloff for editing, and Molly Engelbrecht and Amanda Newsom for reference research and management. This is contribution 2377 from Bodega Marine Laboratory, University of California at Davis.

LITERATURE CITED

- Airoidi L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79:2759–70
- Airoidi L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology* 81:798–814
- Ambrose RF, Nelson BV. 1982. Inhibition of giant kelp recruitment by an introduced brown alga. *Bot. Mar.* 25:265–68

- Andrew NL, Viejo RM. 1998. Ecological limits to the invasion of *Sargassum muticum* in northern Spain. *Aquat. Bot.* 60:251–63
- Arenas F, Sánchez I, Hawkins SJ, Jenkins SR. 2006. The invasibility of marine algal assemblages: Role of functional diversity and identity. *Ecology* 87:2851–61
- Argyrou M, Demetropoulos A, Hadjichristophorou M. 1999. Expansion of the macroalga *Caulerpa racemosa* and changes in softbottom macrofaunal assemblages in Moni Bay, Cyprus. *Oceanol. Acta* 22:517–28
- Balata D, Piazzini L, Cinelli F. 2004. A comparison among assemblages in areas invaded by *Caulerpa taxifolia* and *C. racemosa* on a subtidal Mediterranean rocky bottom. *Mar. Ecol.* 25:1–13
- Bjærke MR, Fredriksen S. 2003. Epiphytic macroalgae on the introduced brown seaweed *Sargassum muticum* (Yendo) Fensholt (Phaeophyceae) in Norway. *Sarsia* 88:353–64
- Boudouresque CF, Briand F, Nolan C. 1994. Introduced species in European coastal waters. *Eur. Comm. Ecosyst. Res. Rep.* 8:76–84
- Boudouresque CF, Lemee R, Mari X, Meinesz A. 1996. The invasive alga *Caulerpa taxifolia* is not a suitable diet for the sea urchin *Paracentrotus lividus*. *Aquat. Bot.* 53:245–50
- Boudouresque CF, Verlaque M. 2002a. Assessing scale and impact of ship-transported alien macrophytes in the Mediterranean Sea. In *CIESM Workshop Monogr. No. 20*, pp. 53–61
- Boudouresque CF, Verlaque M. 2002b. Biological pollution in the Mediterranean Sea: Invasive vs introduced macrophytes. *Mar. Pollut. Bull.* 44:32–38
- Britton-Simmons KH. 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Mar. Ecol. Prog. Ser.* 277:61–78**
- Britton-Simmons KH. 2006. Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. *Oikos* 113:395–401
- Bulleri F, Airolidi L. 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *J. Appl. Ecol.* 42:1063–72
- Bulleri F, Airolidi L, Branca GM, Abbiati M. 2006. Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels. *Mar. Biol.* 148:1213–20
- Buschbaum C, Chapman AS, Saier B. 2006. How an introduced seaweed can affect epibiota diversity in different coastal systems. *Mar. Biol.* 148:743–54
- Byers JE. 2002. Impact of nonindigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97:449–58
- Carlton JT, Geller JB. 1993. Ecological roulette—the global transport of nonindigenous marine organisms. *Science* 261:78–82
- Casas G, Scrosati R, Piriz ML. 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biol. Invasions* 6:411–16

Uses the novel approach of structural equation modeling to elucidate indirect interactions between introduced *Sargassum muticum* and the invaded community.

Highlights the lack of information on introduced species from tropical waters, most notably coral reefs.

- Castilla JC, Uribe M, Bahamonde N, Clarke M, Desqueyroux-Faundez R, et al. 2005. Down under the southeastern Pacific: Marine nonindigenous species in Chile. *Biol. Invasions* 7:213–32
- Ceccherelli G, Campo D. 2002. Different effects of *Caulerpa racemosa* on two co-occurring seagrasses in the Mediterranean. *Bot. Mar.* 45:71–76
- Ceccherelli G, Cinelli F. 1997. Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. *J. Exp. Mar. Biol. Ecol.* 217:165–77
- Ceccherelli G, Cinelli F. 1999a. Effects of *Posidonia oceanica* canopy on *Caulerpa taxifolia* size in a north-western Mediterranean bay. *J. Exp. Mar. Biol. Ecol.* 240:19–36
- Ceccherelli G, Cinelli F. 1999b. A pilot study of nutrient enriched sediments in a *Cymodocea nodosa* bed invaded by the introduced alga *Caulerpa taxifolia*. *Bot. Mar.* 42:409–17
- Ceccherelli G, Piazzzi L, Balata D. 2002. Spread of introduced *Caulerpa* species in macroalgal habitats. *J. Exp. Mar. Biol. Ecol.* 280:1–11
- Ceccherelli G, Piazzzi L, Cinelli F. 2000. Response of the nonindigenous *Caulerpa racemosa* (Forsskål) J. Agardh to the native seagrass *Posidonia oceanica* (L.) Delile: Effect of density of shoots and orientation of edges of meadows. *J. Exp. Mar. Biol. Ecol.* 243:227–40
- Ceccherelli G, Sechi N. 2002. Nutrient availability in the sediment and the reciprocal effects between the native seagrass *Cymodocea nodosa* and the introduced rhizophytic alga *Caulerpa taxifolia*. *Hydrobiologia* 474:57–66
- Chapman AS. 1998. From introduced species to invader: What determines variation in the success of *Codium fragile* ssp. *tomentosoides* (Chlorophyta) in the North Atlantic Ocean? *Helgol. Mar. Res.* 52:277–89
- Chavanich S, Harris LG. 2004. Impact of the non-native macroalga *Codium fragile* (Sur.) Hariot ssp. *tomentosoides* (van Goor) Silva on the native snail *Lacuna vincta* (Montagu, 1803) in the Gulf of Maine. *Veliger* 47:85–90
- Chisholm JRM, Fernex FE, Mathieu D, Jaubert JM. 1997. Wastewater discharge, seagrass decline and algal proliferation on the Cote d'Azur. *Mar. Pollut. Bull.* 34:78–84
- Chisholm JRM, Moulin P. 2003. Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia*. *Limnol. Oceanogr.* 48:787–94
- Coles SL, Eldredge LG. 2002. Nonindigenous species introductions on coral reefs: A need for information. *Pac. Sci.* 56:191–209**
- Conklin EJ, Smith JE. 2005. Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options. *Biol. Invasions* 7:1029–39
- Critchley AT, Ohno M, Largo DB, eds. 2006. *World Seaweed Resources*. Paris, France: UNESCO (DVD-ROM)
- Daehler CC. 1998. The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds. *Biol. Conserv.* 84:167–80
- Davis AR, Benkendorff K, Ward DW. 2005. Responses of common SE Australian herbivores to three suspected invasive *Caulerpa* spp. *Mar. Biol.* 146:859–68

- Delgado O, Rodriguez-Prieto C, Gacia E, Ballesteros E. 1996. Lack of severe nutrient limitation in *Caulerpa taxifolia* (Vahl) C. Agardh, an introduced seaweed spreading over the oligotrophic northwestern Mediterranean. *Bot. Mar.* 39:61–67
- DeWreede RE. 1983. *Sargassum muticum* (Fucales, Phaeophyta)—regrowth and interaction with *Rhodobola larix* (Ceramiales, Rhodophyta). *Phycologia* 22:153–60
- Deyssher L, Norton TA. 1981. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. *J. Exp. Mar. Biol. Ecol.* 56:179–95
- Druehl LD. 1973. Marine transplantations. *Science* 179:12
- Dumay O, Fernandez C, Pergent G. 2002a. Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *J. Mar. Biol. Assoc. UK* 82:379–87
- Dumay O, Pergent G, Pergent-Martini C, Amade P. 2002b. Variations in caulerpenyne contents in *Caulerpa taxifolia* and *Caulerpa racemosa*. *J. Chem. Ecol.* 28:343–52
- Dunstan PK, Johnson CR. 2004. Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. *Oecologia* 138:285–92
- Edgar GJ, Barrett NS, Morton AJ, Samson CR. 2004. Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. *J. Exp. Mar. Biol. Ecol.* 312:67–87
- Eklöf JS, de la Torre Castro M, Adelskold L, Jiddawi NS, Kautsky N. 2005. Differences in macrofaunal and seagrass assemblages in seagrass beds with and without seaweed farms. *Estuar. Coastal Shelf Sci.* 63:385–96
- Farrell P, Fletcher RL. 2006. An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *J. Exp. Mar. Biol. Ecol.* 334:236–43
- Fernex FE, Migon C, Chisholm JRM. 2001. Entrapment of pollutants in Mediterranean sediments and biogeochemical indicators of their impact. *Hydrobiologia* 450:31–46
- Ferrer E, Garreta AG, Ribera MA. 1997. Effect of *Caulerpa taxifolia* on the productivity of two Mediterranean macrophytes. *Mar. Ecol. Prog. Ser.* 149:279–87
- Forrest BM, Taylor MD. 2002. Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. *Biol. Invasions* 4:375–86**
- France KE, Duffy JE. 2006. Consumer diversity mediates invasion dynamics at multiple trophic levels. *Oikos* 113:515–29
- Freshwater DW, Montgomery F, Greene JK, Hamner RM, Williams M, Whitfield PE. 2006. Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. *Biol. Invasions* 8:631–37
- Garbary DJ, Fraser SJ, Hubbard C, Kim KY. 2004. *Codium fragile*: Rhizomatous growth in the *Zostera* thicket of eastern Canada. *Helgol. Mar. Res.* 58:141–46
- Gianguzza P, Airoidi L, Chemello R, Todd CD, Riggio S. 2002. Feeding preferences of *Oxynoe olivacea* (Opisthobranchia: Sacoglossa) among three *Caulerpa* species. *J. Molluscan Stud.* 68:289–90

Recommends Before-After-Control-Impact studies for identifying invasive seaweed impacts along with application of a precautionary management approach.

The single-source database for algal taxonomy and species' distributions.

Asserts that further advancements in remote sensing technology are needed to detect introduced seaweeds over large areas.

- Gollan JR, Wright JT. 2006. Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. *Mar. Freshw. Res.* 57:685–94
- Gribben PE, Wright JT. 2006a. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. *Mar. Ecol. Prog. Ser.* 318:177–85
- Gribben PE, Wright JT. 2006b. Sublethal effects on reproduction in native fauna: are females more vulnerable to biological invasion? *Oecologia* 149:352–61
- Guiry MD, Guiry GM. 2007. *AlgaeBase version 4.2. World-wide electronic publication.* Galway: National Univ. Ireland. <http://www.algaebase.org>**
- Harris LG, Jones AC. 2005. Temperature, herbivory and epibiont acquisition as factors controlling the distribution and ecological role of an invasive seaweed. *Biol. Invasions* 7:913–24
- Harris LG, Mathieson AC. 1999. Patterns of range expansion, niche shift and predator acquisition in *Codium fragile* ssp. *tomentosoides* and *Membranipora membranacea* in the Gulf of Maine. *Rep. NHU-R-99-006*. Durham: NH Sea Grant
- Howarth RW, Sharpley A, Walker D. 2002. Sources of nutrient pollution to coastal waters in the United States: Implications for achieving coastal water quality goals. *Estuaries* 25:656–76
- Inderjit, Chapman DJ, Ranelletti M, Kaushik S. 2006. Invasive marine algae: An ecological perspective. *Bot. Rev.* 72:153–78
- Jaubert JM, Chisholm JRM, Ducrot D, Ripley HT, Roy L, Passeron-Seitre G. 1999. No deleterious alterations in *Posidonia* beds in the Bay of Menton (France) eight years after *Caulerpa taxifolia* colonization. *J. Phycol.* 35:1113–19
- Jaubert JM, Chisholm JRM, Minghelli-Roman A, Marchioretto M, Morrow JH, Ripley HT. 2003. Re-evaluation of the extent of *Caulerpa taxifolia* development in the northern Mediterranean using airborne spectrographic sensing.** *Mar. Ecol. Prog. Ser.* 263:75–82
- Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17:164–70
- Kerswell AP. 2006. Global biodiversity patterns of benthic marine algae. *Ecology* 87:2479–88
- Klein J, Ruitton S, Verlaque M, Boudouresque CF. 2005. Species introductions, diversity and disturbances in marine macrophyte assemblages of the northwestern Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 290:79–88
- Lapointe BE, Barile PJ, Wynne MJ, Yentsch CS. 2005. Reciprocal invasion: Mediterranean native *Caulerpa ollivieri* in the Bahamas supported by human nitrogen enrichment. *Aquat. Invaders* 16:3–5
- Levi F, Francour P. 2004. Behavioural response of *Mullus surmuletus* to habitat modification by the invasive macroalga *Caulerpa taxifolia*. *J. Fish Biol.* 64:55–64
- Levin PS, Coyer JA, Petrik R, Good TP. 2002. Community-wide effects of non-indigenous species on temperate rocky reefs. *Ecology* 83:3182–93
- Littler MM, Littler DS, Titlyanov EA. 1991. Producers of organic matter on tropical reefs and their relative dominance. *Mar. Biol.* 6:3–14
- Lockwood JL. 1999. Using taxonomy to predict success among introduced avifauna: Relative importance of transport and establishment. *Conserv. Biol.* 13:560–67

- Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, et al. 2006. Biological invasions: Recommendations for US policy and management. *Ecol. Appl.* 16:2035–54
- Longepierre S, Robert A, Levi F, Francour P. 2005. How an invasive alga species (*Caulerpa taxifolia*) induces changes in foraging strategies of the benthivorous fish *Mullus surmuletus* in coastal Mediterranean ecosystems. *Biodivers. Conserv.* 14:365–76
- Lowe S, Browne M, Boudjelas S, De Poorter M. 2004. *100 of the World's Worst Invasive Alien Species*. Auckland, NZ: Univ. Auckland
- Maggs CA, Stegenga H. 1999. Red algal exotics on North Sea coasts. *Helgol. Mar. Res.* 52:243–58
- Mann K. 1973. Seaweeds: Their productivity and strategy for growth. *Science* 182:975–81**
- Mathieson AC, Dawes CJ, Harris LG, Hehre EJ. 2003. Expansion of the Asiatic green alga *Codium fragile* ssp. *tomentosoides* in the Gulf of Maine. *Rhodora* 105:1–53
- Meinesz A. 1999. *Killer Algae*, ed. D Simberloff. Chicago, IL: Univ. Chicago Press**
- Naylor RL, Williams SL, Strong DR. 2001. Aquaculture—A gateway for exotic species. *Science* 294:1655–56
- Occhipinti Ambrogi A. 2000. Biotic invasions in a Mediterranean lagoon. *Biol. Invasions* 2:165–76
- Occhipinti Ambrogi A, Savini D. 2003. Biological invasions as a component of global change in stressed marine ecosystems. *Mar. Pollut. Bull.* 46:542–51
- Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, et al. 2002. No longer the pristine confines of the world ocean: A survey of exotic marine species in the southwestern Atlantic. *Biol. Invasions* 4:115–43
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, et al. 2006. A global crisis for seagrass ecosystems. *BioScience* 56:987–96
- Padilla DK, Williams SL. 2004. Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Front. Ecol. Environ.* 2:131–38
- Parker JD, Burkepille DE, Hay ME. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–61
- Pedersen MF, Stæhr PA, Wernberg T, Thomsen MS. 2005. Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark—Implications of species replacements on turnover rates. *Aquat. Bot.* 83:31–47
- Piazzi L, Balata D, Cecchi E, Cinelli F. 2003a. Co-occurrence of *Caulerpa taxifolia* and *C. racemosa* in the Mediterranean Sea: Interspecific interactions and influence on native macroalgal assemblages. *Cryptogam. Algol.* 24:233–43
- Piazzi L, Ceccherelli G. 2002. Effects of competition between two introduced *Caulerpa*. *Mar. Ecol. Prog. Ser.* 225:189–95
- Piazzi L, Ceccherelli G. 2006. Persistence of biological invasion effects: Recovery of macroalgal assemblages after removal of *Caulerpa racemosa* var. *cylindracea*. *Estuar. Coastal Shelf Sci.* 68:455–61

A classical paper documenting the global importance of seaweeds as marine primary producers.

Raises global consciousness regarding *Caulerpa taxifolia*, providing the impetus for its eradication in California and management in Australia.

- Piazzì L, Ceccherelli G, Balata D, Cinelli F. 2003b. Early patterns of *Caulerpa racemosa* recovery in the Mediterranean Sea: The influence of algal turfs. *J. Mar. Biol. Assoc. UK* 83:27–29
- Piazzì L, Ceccherelli G, Cinelli F. 2001. Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. *Mar. Ecol. Prog. Ser.* 210:149–59
- Piazzì L, Cinelli F. 2003. Evaluation of benthic macroalgal invasion in a harbour area of the western Mediterranean Sea. *Eur. J. Phycol.* 38:223–31
- Prince JS, Leblanc WG. 1992. Comparative feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for the invasive seaweed *Codium fragile* ssp. *tomentosoides* (Chlorophyceae) and 4 other seaweeds. *Mar. Biol.* 113:159–63
- Ribera MA, Boudouresque CF. 1995. Introduced marine plants, with special reference to macroalgae: mechanisms and impact. In *Progress in Phycological Research*, ed. FE Round, DJ Chapman, pp. 187–268. Bristol, UK: Biopress
- Ribera Siguan MA. 2002. Review of non-native marine plants in the Mediterranean Sea. In *Invasive Aquatic Species of Europe—Distribution, Impacts and Management*, ed. E Leppäkoski, S Gollasch, S Olenin, pp. 291–310. Dordrecht: Kluwer Acad.
- Ribera Siguan MA. 2003. Pathways of biological invasions of marine plants. In *Invasive Species: Vectors and Management Strategies*, ed. GM Ruiz, JT Carlton, pp. 183–226. Washington, DC: Island Press
- Ruiz GM, Fofonoff P, Hines AH, Grosholz ED. 1999. Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. *Limnol. Oceanogr.* 44:950–72
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annu. Rev. Ecol. Syst.* 31:481–531
- Sala E, Boudouresque CF. 1997. The role of fishes in the organization of a Mediterranean sublittoral community. 1. Algal communities. *J. Exp. Mar. Biol. Ecol.* 212:25–44
- Sánchez I, Fernández C. 2005. Impact of the invasive seaweed *Sargassum muticum* (Phaeophyta) on an intertidal macroalgal assemblage. *J. Phycol.* 41:923–30
- Sánchez I, Fernández C. 2006. Resource availability and invasibility in an intertidal macroalgal assemblage. *Mar. Ecol. Prog. Ser.* 313:85–94
- Sánchez I, Fernández C, Arrontes J. 2005. Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). *J. Phycol.* 41:942–49
- Sant N, Delgado O, Rodríguez-Prieto C, Ballesteros E. 1996. The spreading of the introduced seaweed *Caulerpa taxifolia* (Vahl) C. Agardh in the Mediterranean sea: Testing the boat transportation hypothesis. *Bot. Mar.* 39:427–30
- Sax DF, Kinlan BP, Smith KF. 2005. A conceptual framework for comparing species assemblages in native and exotic habitats. *Oikos* 108:457–64
- Schaffelke B, Evers D, Walhorn A. 1995. Selective grazing of the isopod *Idotea baltica* between *Fucus evanescens* and *F. vesiculosus* from Kiel Fjord (western Baltic). *Mar. Biol.* 124:215–18
- Schaffelke B, Smith JE, Hewitt CL. 2006. Introduced macroalgae—a growing concern. *J. Appl. Phycol.* 18:529–41

- Scheibling RE, Anthony SX. 2001. Feeding, growth and reproduction of sea urchins (*Strongylocentrotus droebachiensis*) on single and mixed diets of kelp (*Laminaria* spp.) and the invasive alga *Codium fragile* ssp. *tomentosoides*. *Mar. Biol.* 139:139–46
- Scheibling RE, Gagnon P. 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweed. *Mar. Ecol. Prog. Ser.* 325:1–14
- Schmidt AL, Scheibling RE. 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. *Bot. Mar.* 49:315–30
- Schueller GH, Peters AF. 1994. Arrival of *Fucus evanescens* (Phaeophyceae) in Kiel Bight (western Baltic). *Bot. Mar.* 37:471–77
- Secord D. 2003. Biological control of marine invasive species: cautionary tales and land-based lessons. *Biol. Invasions* 5:117–31
- Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: Invasional meltdown? *Biol. Invasions* 1:21–32
- Smith CM, Walters LJ. 1999. Fragmentation as a strategy for *Caulerpa* species: Fates of fragments and implications for management of an invasive weed. *Mar. Ecol. Prog. Ser.* 20:307–19
- Smith JE, Most R, Sauvage T, Hunter C, Squair C, Conklin E. 2004. Ecology of the invasive red alga *Gracilaria salicornia* in Waikiki and possible mitigation strategies. *Pac. Sci.* 58:325–43
- Stæhr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D. 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Mar. Ecol. Prog. Ser.* 207:79–88
- Stam WT, Olsen JL, Zaleski SF, Murray SN, Brown KR, Walters LJ. 2006. A forensic and phylogenetic survey of *Caulerpa* species (Caulerpales, Chlorophyta) from the Florida coast, local aquarium shops, and e-commerce: Establishing a proactive baseline for early detection. *J. Phycol.* 42:1113–24**
- Steen H, Rueness J. 2004. Comparison of survival and growth in germlings of six fucoid species (Fucales, Phaeophyceae) at two different temperature and nutrient levels. *Sarsia* 89:175–83
- Steneck RS, Dethier MN. 1994. A functional-group approach to the structure of algal-dominated communities. *Oikos* 69:476–98
- Stimson J, Larned ST, Conklin E. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19:343–57
- Strong JA, Dring MJ, Maggs CA. 2006. Colonisation and modification of soft substratum habitats by the invasive macroalga *Sargassum muticum*. *Mar. Ecol. Prog. Ser.* 321:87–97
- Sumi CBT, Scheibling RE. 2005. Role of grazing by sea urchins *Strongylocentrotus droebachiensis* in regulating the invasive alga *Codium fragile* ssp. *tomentosoides* in Nova Scotia. *Mar. Ecol. Prog. Ser.* 292:203–12
- Terrados J, Marbà N. 2006. Is the vegetative development of the invasive chlorophycean, *Caulerpa taxifolia*, favored in sediments with a high content of organic matter? *Bot. Mar.* 49:331–38

Exemplifies the growing use of molecular techniques to determine the identity, origin, and vector for an introduced seaweed.

- Thibaut T, Meinesz A, Amade P, Charrier S, De Angelis K, et al. 2001. *Elysia subornata* (Mollusca) a potential control agent of the alga *Caulerpa taxifolia* (Chlorophyta) in the Mediterranean Sea. *J. Mar. Biol. Assoc. UK* 81:497–504
- Thomsen MS, McGlathery KJ, Tyler AC. 2006a. Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. *Estuar. Coasts* 29:465–73
- Thomsen MS, Wernberg T, Stæhr PA, Pedersen MF. 2006b. Spatio-temporal distribution patterns of the invasive macroalga *Sargassum muticum* within a Danish *Sargassum* bed. *Helgol. Mar. Res.* 60:50–58
- Thornber CS, Kinlan BP, Graham MH, Stachowicz JJ. 2004. Population ecology of the invasive kelp *Undaria pinnatifida* in California: Environmental and biological controls on demography. *Mar. Ecol. Prog. Ser.* 268:69–80
- Trowbridge C. 2006. A global proliferation of non-native marine and brackish macroalgae. See Critchley et al. 2006
- Trowbridge CD. 1995. Establishment of green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: Current distribution and invertebrate grazers. *J. Ecol.* 83:949–65
- Trowbridge CD. 2001. Coexistence of introduced and native congeneric algae: *Codium fragile* and *C. tomentosum* on Irish rocky intertidal shores. *J. Mar. Biol. Assoc. UK* 81:931–37
- Trowbridge CD, Todd CD. 2001. Host-plant change in marine specialist herbivores: Ascoglossan sea slugs on introduced macroalgae. *Ecol. Monogr.* 71:219–43
- Valentine JP, Johnson CR. 2003. Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. *J. Exp. Mar. Biol. Ecol.* 295:63–90
- Valentine JP, Johnson CR. 2004. Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. *Mar. Freshw. Res.* 55:223–30
- Valentine JP, Johnson CR. 2005. Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. *Mar. Ecol. Prog. Ser.* 285:43–55
- Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42:1105–18
- Viejo RM. 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquat. Bot.* 64:131–49
- Vincent C, Mouillot D, Lauret M, Do Chi T, Troussellier M, Aliaume C. 2006. Contribution of exotic species, environmental factors and spatial components to the macrophyte assemblages in a Mediterranean lagoon (Thau lagoon, Southern France). *Ecol. Model.* 193:119–31
- Vroom PS, Smith CM. 2001. The challenge of siphonous green algae. *Am. Sci.* 89:524–31
- Walker TL, Collet C, Purton S. 2005. Algal transgenics in the genomic era. *J. Phycol.* 41:1077–93
- Walters LJ, Brown KR, Stam WT, Olsen JL. 2006. E-commerce and *Caulerpa*: Unregulated dispersal of invasive species. *Front. Ecol. Environ.* 4:75–79

- Wernberg T, Thomsen MS, Stæhr PA, Pedersen MF. 2004. Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). *Helgol. Mar. Res.* 58:154–61
- Wikström SA, Kautsky L. 2004. Invasion of a habitat-forming seaweed: effects on associated biota. *Biol. Invasions* 6:141–50
- Wikström SA, Steinarsdóttir MB, Kautsky L, Pavia H. 2006. Increased chemical resistance explains low herbivore colonization of introduced seaweed. *Oecologia* 148:593–601
- Williams SL, Grosholz ED. 2002. Preliminary reports from the *Caulerpa taxifolia* invasion in southern California. *Mar. Ecol. Prog. Ser.* 233:307–10
- Wright JT, Davis AR. 2006. Demographic feedback between clonal growth and fragmentation in an invasive seaweed. *Ecology* 87:1744–54
- York PH, Booth DJ, Glasby TM, Pease BC. 2006. Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. *Mar. Ecol. Prog. Ser.* 312:223–34
- Zar JH. 1999. *Biostatistical Analysis*. Upper Saddle River, NJ: Prentice Hall
- Zemke-White WL, Ohno M. 1999. World seaweed utilization: An end of the century summary. *J. Appl. Phycol.* 11:369–76
- Zemke-White WL, Smith JE. 2006. Environmental impacts of seaweed farming in the tropics. See Critchley et al. 2006
- Züljevic A, Thibaut T, Elloukal H, Meinesz A. 2001. Sea slug disperses the invasive *Caulerpa taxifolia*. *J. Mar. Biol. Assoc. UK* 81:343–44

RELATED RESOURCES

- Colautti RI, Bailey SA, van Overdijk CDA, Amundsen K, MacIsaac HJ. 2006. Characterised and projected costs of nonindigenous species in Canada. *Biol. Invasions* 8:45–59
- Int. Council. Explor. Sea. 1995. *Code of Practice on the Introductions and Transfers of Marine Organisms*, 1994. Copenhagen: ICES
- Neill PE, Alcalde O, Faugeron S, Navarrete SA, Correa JA. 2006. Invasion of *Codium fragile* ssp. *tomentosoides* in northern Chile: a new threat for *Gracilaria* farming. *Aquaculture* 259:202–10
- Van Beukering PJH, Cesar H. 2004. Ecological economic modeling of coral reefs: evaluating tourist overuse at Hanauma Bay and algae blooms at the Kihei coast, Hawai'i. *Pac. Sci.* 58:243–51



Contents

Evolution of Animal Photoperiodism <i>William E. Bradshaw and Christina M. Holzapfel</i>	1
Virus Evolution: Insights from an Experimental Approach <i>Santiago F. Elena and Rafael Sanjuán</i>	27
The Social Lives of Microbes <i>Stuart A. West, Stephen P. Diggle, Angus Buckling, Andy Gardner, and Asleigh S. Griffin</i>	53
Sexual Selection and Speciation <i>Michael G. Ritchie</i>	79
Kin Selection and the Evolutionary Theory of Aging <i>Andrew F.G. Bourke</i>	103
Climate Change and Invasibility of the Antarctic Benthos <i>Richard B. Aronson, Sven Thatje, Andrew Clarke, Lloyd S. Peck, Daniel B. Blake, Cheryl D. Wilga, and Brad A. Seibel</i>	129
Spatiotemporal Dimensions of Visual Signals in Animal Communication <i>Gil G. Rosenthal</i>	155
Gliding and the Functional Origins of Flight: Biomechanical Novelty or Necessity? <i>Robert Dudley, Greg Byrnes, Stephen P. Yanoviak, Brendan Borrell, Rafe M. Brown, and Jimmy A. McGuire</i>	179
How Mutational Networks Shape Evolution: Lessons from RNA Models <i>Matthew C. Cowperthwaite and Lauren Ancel Meyers</i>	203
How Does It Feel to Be Like a Rolling Stone? Ten Questions about Dispersal Evolution <i>Ophélie Ronce</i>	231
Exploring Cyanobacterial Mutualisms <i>Kayley M. Usber, Birgitta Bergman, and John A. Raven</i>	255

Human Impacts in Pine Forests: Past, Present, and Future <i>David M. Richardson, Philip W. Rundel, Stephen T. Jackson, Robert O. Teskey, James Aronson, Andrzej Bytnerowicz, Michael J. Wingfield, and Šerban Procheş</i>	275
Chemical Complexity and the Genetics of Aging <i>Scott D. Pletcher, Hadise Kabil, and Linda Partridge</i>	299
A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds <i>Susan L. Williams and Jennifer E. Smith</i>	327
The Very Early Stages of Biological Evolution and the Nature of the Last Common Ancestor of the Three Major Cell Domains <i>Arturo Becerra, Luis Delaye, Sara Islas, and Antonio Lazcano</i>	361
Functional Versus Morphological Diversity in Macroevolution <i>Peter C. Wainwright</i>	381
Evolutionary Game Theory and Adaptive Dynamics of Continuous Traits <i>Brian J. McGill and Joel S. Brown</i>	403
The Maintenance of Outcrossing in Predominantly Selfing Species: Ideas and Evidence from Cleistogamous Species <i>Christopher G. Oakley, Ken S. Moriuchi, and Alice A. Winn</i>	437
Sympatric Speciation: Models and Empirical Evidence <i>Daniel I. Bolnick and Benjamin M. Fitzpatrick</i>	459
The Evolution of Color Polymorphism: Crypticity, Searching Images, and Apostatic Selection <i>Alan B. Bond</i>	489
Point, Counterpoint: The Evolution of Pathogenic Viruses and their Human Hosts <i>Michael Worobey, Adam Bjork, and Joel O. Wertheim</i>	515
The Evolution of Resistance and Tolerance to Herbivores <i>Juan Núñez-Farfán, Juan Fornoni, and Pedro Luis Valverde</i>	541
Plant-Animal Mutualistic Networks: The Architecture of Biodiversity <i>Jordi Bascompte and Pedro Jordano</i>	567
Gene Flow and Local Adaptation in Trees <i>Outi Savolainen, Tanja Pyhäjärvi, and Timo Knürr</i>	595
The Evolution of Multicellularity: A Minor Major Transition? <i>Richard K. Grosberg and Richard R. Strathmann</i>	621
Developmental Genetics of Adaptation in Fishes: The Case for Novelty <i>J.T. Streebman, C.L. Peichel, and D.M. Parichy</i>	655

Terrestrial Carbon–Cycle Feedback to Climate Warming <i>Yiqi Luo</i>	683
Shortcuts for Biodiversity Conservation Planning: The Effectiveness of Surrogates <i>Ana S.L. Rodrigues and Thomas M. Brooks</i>	713
Understanding the Effects of Marine Biodiversity on Communities and Ecosystems <i>John J. Stachowicz, John F. Bruno, and J. Emmett Duffy</i>	739
Stochastic Dynamics of Plant–Water Interactions <i>Gabriel Katul, Amilcare Porporato, and Ram Oren</i>	767
Evolutionary Endocrinology: The Developing Synthesis between Endocrinology and Evolutionary Genetics <i>Anthony J. Zera, Lawrence G. Harshman, and Tony D. Williams</i>	793
The Role of Behavior in the Evolution of Spiders, Silks, and Webs <i>Fritz Vollrath and Paul Selden</i>	819
Applications of Flow Cytometry to Evolutionary and Population Biology <i>Paul Kron, Jan Suda, and Brian C. Husband</i>	847

Indexes

Cumulative Index of Contributing Authors, Volumes 34–38	877
Cumulative Index of Chapter Titles, Volumes 34–38	881

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>