Native pipefish *Entelurus aequoreus* are promoted by the introduced seaweed *Sargassum muticum* in the northern Wadden Sea, North Sea

Patrick Polte¹, ², *, Christian Buschbaum¹

¹Alfred Wegener Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstr. 43, 25992 List, Germany
²Present address: Northwest Fisheries Science Center, NOAA Fisheries, 2725 Montlake Blvd. East, Seattle, Washington 98112-2097, USA

ABSTRACT: After the major loss of eelgrass habitats in the 1930s the snake pipefish *Entelurus aequoreus* was considered to be rare in the Wadden Sea (south-eastern North Sea, German Bight). We hypothesize that a sudden increase in pipefish abundance observed in the area since 2004 is related to new habitats provided by the introduced Japanese seaweed *Sargassum muticum*. SCUBA observations conducted near the Island of Sylt during July 2006 showed that approximately every second *S. muticum* thallus was inhabited by *E. aequoreus*, whereas no pipefish could be found on sedimentary areas dominating the Wadden Sea. In a field experiment, we removed thalli from a *S. muticum* bed and transplanted them to an unvegetated site and to the donor *S. muticum* bed, respectively. Nine days after the transplantation, abundances of pipefish per thallus were almost equally high within all transplanted *S. muticum* units at vegetated and originally unvegetated sites. Abundances of *E. aequoreus* in transplanted thalli did not significantly differ from those found in unaffected control thalli located in the donor *S. muticum* bed. To explain high pipefish densities within *S. muticum* beds we sampled the zooplankton community inside and outside the *S. muticum* bed and compared it with gut contents of pipefish. Zooplankton densities were significantly higher inside the *S. muticum* bed. Harpacticoid copepods were the dominant group associated with *S. muticum* and also represented the major prey of *E. aequoreus*. We conclude that stocks of *E. aequoreus* are promoted by *S. muticum* beds since they benefit from higher food supply during the spawning season, probably in addition to increased shelter by habitat complexity. Results of the present study suggest that introductions of habitat-forming species such as *S. muticum* may cause beneficial effects on abundance and diversity of native species.

KEY WORDS: Introduced seaweed · Pipefish · *Sargassum muticum* · *Entelurus aequoreus* · Zooplankton · Wadden Sea · North Sea

INTRODUCTION

In coastal ecosystems biogenic habitats composed of macrophytes such as seagrasses are generally known to increase abundance and species diversity of associated fish communities (e.g. Pollard 1984, Jackson et al. 2001, Franco et al. 2006). In the Wadden Sea, shallow-water fish diversity is considered to have declined since the major loss of subtidal seagrass habitats during the 1930s (Wolff 2000, Polte 2004), when an infec-

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*Email: patrick.polte@noaa.gov*
complex macrophyte habitats in the shallow subtidal zone (Berg et al. 1996). During fish surveys carried out in 2003 on intertidal seagrass beds (Zostera noltii), mussel beds (Mytilus edulis) and sand flats, as well as in subtidal areas where Z. marina formerly occurred and which were unvegetated at the time of sampling, none of the named fish species could be found (Polte 2004, Polte & Asmus 2006). However, since 2004 S. spinachia and E. aequoreus could be observed more frequently in the northern Wadden Sea (P. Polte & C. Buschbaum unpubl. data). Snake pipefish E. aequoreus in particular was found in exceptionally high abundances in the north-eastern Atlantic Ocean during the last 5 yr (Kirby et al. 2006, Lindley et al. 2006, Harris et al. 2007, 2008, Kloppmann & Ulleweit 2007). The reason for the strong increase of the snake pipefish population has been attributed so far to global warming and a rise in sea surface temperatures that benefit reproduction and survival of larvae (Kirby et al. 2006, Lindley et al. 2006).

Based on observations in the northern Wadden Sea (south-eastern North Sea), we assume that the increasing success of the introduced Japanese seaweed Sargassum muticum (Yendo) might also represent a key factor promoting Entelurus aequoreus by providing important habitats, especially during the spawning season, when males that conduct parental care find shelter and an enriched food supply within the S. muticum beds. Sargassum muticum is highly invasive and, currently, has an almost worldwide distribution. Probably as a result of oyster Crassostrea gigas Thunberg aquaculture activities, it became introduced to northern Europe in 1976. From the English Channel S. muticum rapidly spread north- and southward. Because of its successful reproductive strategy by self-fertilisation (Fletcher 1975, Norton 1976, 1977) and efficient dispersal mechanism by floating thalli, its current distribution reaches from Portugal to Scandinavia (Druehl 1973, Critchley 1983, Rueness 1989, Karlsson & Loo 1999, Wolff 2005). After establishment, densities of S. muticum have strongly increased along European coasts (e.g. Critchley et al. 1987, Karlsson & Loo 1999, Staehr et al. 2000).

Sargassum muticum became established in the southern range of the Wadden Sea in 1980, where it was first found at the Dutch island of Texel. Since 1993, S. muticum can regularly be found near the Island of Sylt (Germany) in the northern Wadden Sea (Kornmann & Sahling 1994). In this area, S. muticum grows in the shallow subtidal zone at the particular tidal level where eelgrass Zostera marina occurred before stocks vanished. In the sedimentary environment of the Wadden Sea, S. muticum preferentially settles on epibenthic molluscs such as native blue mussels Mytilus edulis and the introduced Pacific oyster Crassostrea gigas (Buschbaum 2005, Buschbaum et al. 2006). In cold waters S. muticum is pseudo-perennial. The lateral branches detach in summer and early autumn, leaving a short perennial stipe from which thalli regenerate during the following spring (e.g. Jephson & Gray 1977) and may achieve a length of >4 m during summer. Other habitat-forming algae are very rare in the subtidal zone of the Wadden Sea. Hence, S. muticum with its long and complex thalli might serve as a compensatory habitat to native fishes that have been associated with seagrass habitats provided that those fish species are still present on the North Sea scale. Thus, we hypothesised, that: (1) when S. muticum occurs in the shallow subtidal zone it will become inhabited by snake pipefish and (2) the density of planktonic prey is significantly higher within S. muticum beds compared to unvegetated areas.

MATERIALS AND METHODS

Study sites. Studies were conducted on the east coast of the Island of Sylt in the northern Wadden Sea (North Sea) (Fig. 1). A shallow tidal basin is formed by the mainland and the islands of Sylt (Germany) and Rømø (Denmark). Along the tidal watersheds the Sylt–Rømø Bight is nearly closed by causeways connecting the islands with the mainland. A single inlet opens the bight to the open North Sea. Tides are semi-diurnal, with an average amplitude of about 2 m. Salinity ranges seasonally from 28 in winter to 32 in summer. During the vegetation period of Sargassum muticum from February to August, water temperatures vary seasonally from 1 to 20°C. During the investigation period in July 2006, the mean water temperature was 18°C. Mean water depth in the investigated areas ranged from 0.5 m (mean low tide line) to 2 m (mean high tide line).

The intertidal and shallow subtidal zone of the Sylt–Rømø Bight is dominated by bare sandy to muddy sediments. Today, seagrass beds are limited to the intertidal zone and dominated by the dwarf seagrass Zostera noltii, Hornemann, covering approximately 12% of tidal flats (Gätje & Reise 1998). Mussel beds (Mytilus edulis) used to cover 0.3% of the intertidal zone (Gätje & Reise 1998), but may show interannual variations. However, during the last 3 yr, they have become increasingly invaded by the Pacific oyster Crassostrea gigas (Diederich 2006), leading to a shift in landscape from mussel beds to oyster reefs. Introduced by oyster aquaculture, Sargassum muticum has spread in the shallow subtidal zone since 1993 in the range of mussel beds, oyster reefs and breakwaters (Kornmann & Sahling 1994, Buschbaum 2005, Buschbaum et al. 2006). Studies were conducted in a S. muticum bed
located in the subtidal zone on the northern side of Koenigshafen Bay (a shallow subsystem of the Sylt-Rømø Bight) and on unvegetated soft sediments located about 3.5 km south, in the reach of a sheltering breakwater (List Breakwater), off the village of List (Fig. 1). This site was chosen because it fulfils the habitat requirements of *S. muticum* more closely than exposed sand flats and was, therefore, considered to bring the experimental setup as close to natural conditions as possible.

**Density and biomass of Sargassum muticum.** On 10 July 2006, abundance and biomass of *Sargassum muticum* thalli were measured in a seaweed bed that was used as a donor area for experimental transplantation of *S. muticum* to study pipefish settlement (Fig. 1C, Site 1). Densities of thalli were counted in 3 × 3 m plots (n = 20), randomly chosen and defined by tape measure. Thalli were collected randomly (n = 10). The algae were detached from their substrata (oysters *Crassostrea gigas* and mussels *Mytilus edulis*), placed in a bucket (of known weight) and weighed (g fresh wt) using a spring balance. Additionally, the length of each thallus was recorded using a tape measure. Additionally, the length of each thallus was recorded using a tape measure.

**Sargassum muticum transplantation experiment.** To test the hypothesis that Wadden Sea areas will become inhabited by snake pipefish when *S. muticum* is present, *S. muticum* thalli (n = 20) were randomly removed from the *S. muticum* bed. Afterwards, thalli were detached from the substrata and fresh wt and length were recorded. The thalli were attached to metal poles using cable ties fixed at the thallus’ holdfast. Each unit was equipped with a small number tag fixed to the pole; 10 of the thalli were transplanted a distance of 2 km to the originally unvegetated site at List Breakwater and to a tidal level the same as that at the donor *S. muticum* bed.

Ten thalli attached to metal poles were re-transplanted to the donor *Sargassum muticum* bed to estimate transplantation effects. As control units, another 10 thalli located within the donor *S. muticum* bed were randomly chosen and not handled, except that number tags were fixed on the alga’s holdfast right at the oyster substrate.

On 19 July, 9 d after transplanting the thalli, the abundance of pipefish on transplanted and control units was examined by SCUBA during high tide. Additionally, on unvegetated sandy sediments at List Breakwater, 5 replicate 30 m transects were controlled for the occurrence of pipefish.

Due to the experimental setup, the abundance of pipefish could not be measured per area directly. Instead, abundance was measured as the number of fish per *Sargassum muticum* thallus. Since *Entelurus aequoreus* shows minimal escape behaviour, especially when hiding camouflaged beneath the algae, fish per transplanted thallus could reliably be counted *in situ*. Pipefish abundance per area could be calculated secondarily from fish abundance per thallus and density of thalli per area. Specimens of *E. aequoreus* found near transplanted and control thalli were examined for eggs externally adhered to the trunk of male fish.

**Analyses of pipefish gut contents.** Individuals of *Entelurus aequoreus* were randomly collected within the *Sargassum muticum* bed (n = 8). They were taken to the laboratory where total length and fresh wt were measured. Stomach contents were removed, diluted in seawater and brought into a plankton counting chamber. Organisms found in each stomach were counted and identified to taxonomic order. Fragmented organisms were quantified by counting only the heads.

**Prey densities in the field.** To investigate whether *Sargassum muticum* beds may provide an increased food supply to pipefish during the spawning season, the density of prey fauna within the Koenigshafen Bay *S. muticum* bed was compared to that of adjacent unvegetated areas located at the same tidal level (distance: approximately 20 m). During incoming tide a
A plankton net of 1.60 m length and a diameter of 50 cm (mesh size: 250 µm) was brought to the bottom by a SCUBA diver. The ring frame of the net was carefully moved underneath the bivalve substrate, and the net was pulled vertically over single, submerged S. muticum thalli (n = 6) (almost as long as the height of the water column) from the bottom to the water surface (depth: 1.60 m). At the surface, prior to removing the S. muticum thallus from the net, the thallus was washed 3 times to remove adherent fauna. Outside the S. muticum bed a similar technique was conducted on unvegetated sediment, whereby the net was moved from the bottom to the surface over the same distance as inside the algal bed (n = 6). The sampled water volume inside and outside the S. muticum bed was 0.3 m³ (area of the net opening = 0.2 m² × sampling distance = 1.6 m). Organisms were washed out of the removable cylinder attached to the bottom of the plankton net and fixed in 10% formalin. Organisms from vegetated and unvegetated areas were identified to taxonomic order. Due to the sampling technique used, the term ‘zooplankton’ is used here, although a number of orders caught are usually found close to the sea floor and might also be referred to as hypoplankton or epibenthos.

**Data analysis.** Results of quantitative assessments are presented as arithmetic means with standard errors (±SE). Statistical effects were tested for significance using a 1-way analyses of variance (ANOVA). Datasets were tested for homoscedasticity by Cochran’s test and transformed using log(x + 1) if necessary to fulfill the assumptions for ANOVA. Effects between single treatments of the Sargassum muticum transplantation experiment were analysed using post hoc Tukey’s honestly significant differences (HSD) test. Statistical significance was assumed if the p-level was <0.05.

**RESULTS**

**Sargassum muticum** density and biomass

In the investigated Sargassum muticum bed, mean density (±SE) of thalli was 7 ± 0.05 per 10 m². Thalli had a mean length of 1.4 ± 0.1 m and a mean fresh wt of 0.47 ± 0.05 kg. The thalli transplanted during the experiment showed no significant differences with respect to length and weight (thallus length: ANOVA p = 0.3, df = 2, F = 1.2; thallus fresh wt: ANOVA p = 0.5, df = 2, F = 0.7).

**Abundance of Entelurus aequoreus**

No individuals of Entelurus aequoreus could be found on the unvegetated transects at List Breakwater (Fig. 1). In the Sargassum muticum bed at Koenigshafen Bay (Fig. 1), the abundance of E. aequoreus per thallus in unaffected control thalli was 0.6 ± 0.2 ind. thallus⁻¹. With a given S. muticum density of 7 thalli per 10 m² (see above), abundance of E. aequoreus corresponds to 4.2 ind. per 10 m². At the unvegetated site at List Breakwater, mean abundance of pipefish in transplanted S. muticum thalli was 0.6 ± 0.2 thallus⁻¹. In the transplanted thalli located within the donor S. muticum bed 0.5 ± 0.2 ind. thallus⁻¹ were found (Fig. 2). Pipefish abundances in the experimental treatments showed no significant differences overall (ANOVA, p = 0.9, df = 2, F = 0.05).

Of all pipefish found in transplanted and control Sargassum muticum thalli during the investigation period, 57% were males carrying eggs adhered to their trunk. Note: Beside Entelurus aequoreus, 2 specimens of the sea stickleback Spinachia spinachia were observed inhabiting the transplanted S. muticum thalli, whereas none of these fish were observed at the unvegetated control site.

**Composition of pipefish diet**

Specimens of Entelurus aequoreus sampled for analysis of gut contents had a mean body length of 28.8 ± 0.9 cm and a mean fresh wt of 2.9 ± 0.3 g. Harpacticoid copepods represented by far the majority of prey organisms found in the guts of pipefish from the Sargassum muticum bed. Barnacle and fish larvae, as well as amphipods and mysidaceans, were also found, but in comparably lower percentages (Table 1). Numerical mean abundances of prey groups per fish gut (n = 8) were as follows—harpacticoid copepods:
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74.8 ± 20.9, barnacle (cypris) larvae: 2.4 ± 0.8, fish larvae: 1.4 ± 0.7, amphipods: 1.1 ± 0.5 and mysidaceans: 0.5 ± 0.2.

### Density of zooplankton groups associated with *Sargassum muticum*

The zooplankton sampled in vegetated and unvegetated areas was dominated by copepod and amphipod crustaceans, as well as by planktonic stages of benthic larvae (meroplankton) such as polychaetes, gastropods, bivalves and balanids (Table 2). With 40.8 ± 3.9 ind. per 0.3 m³, the mean density of zooplankton in total was significantly lower in the unvegetated area adjacent to the *Sargassum muticum* bed (p = 0.001, df = 1, F = 21.2) than inside the bed where the total density was 768 ± 158.5 ind. per 0.3 m³. This is also true for all taxonomic groups. Numbers of copepods, amphipods and benthos larvae were all significantly higher in the *S. muticum* bed compared to unvegetated areas (Fig. 3) (copepods: p = 0.001, df = 1, F = 22.0; amphipods: p < 0.001, df = 1, F = 12.02; benthos larvae: p = 0.006, df = 1, F = 98.7). Cypris stages of barnacle larvae (Balanidae) were the only group that showed slightly lower abundances inside *S. muticum* than on unvegetated areas. However, numbers of barnacle larvae found were very low, and differences were not significant (p = 0.3, df = 1, F = 1.4).

### DISCUSSION

Results of the experimental transplantation of *Sargassum muticum* indicate that originally unvegetated areas where snake pipefish were absent became inhabited rapidly after *Sargassum* thalli were artificially introduced. In that area, abundance of *Entelurus aequoreus* reached the same level as in the donor *S. muticum* bed (~1 fish per 2 thalli) within a little more than a week. The process of transplantation and the way thalli were artificially fixed at the site are not considered to have affected the results, since no difference in pipefish abundance could be observed among unaffected control thalli and re-transplants within the original *S. muticum* bed. Sex distribution of fish could not be assessed reliably *in situ*. In contrast to many syngnathid species in which males carry the eggs within a brood pouch, males of *E. aequoreus* carry the eggs externally adhered to their trunk (Vincent et al. 1995). Thus, egg-carrying males could easily be identified *in situ*. They made up 57% of total individuals found during the investigation period. This finding suggests that the vegetation period of *S. muticum* in the Wadden Sea from February to August coincides with the spawning season of *E. aequoreus*, which might point out a significant role of *S. muticum* habitats during pipefish reproduction, a sensitive phase in the fish’s life cycle.

The density of planktonic prey, such as harpacticoid copepods, was significantly increased inside the *Sar-
the plankton community inside the strate that the harpacticoid copepods that dominated spectrum of potential prey. However, they demonstrate biased and are not suggested to cover the entire spectrum of potential prey. However, they demonstrate that the harpacticoid copepods that dominated the plankton community inside the S. muticum bed are a suitable food for pipefish and are extensively preyed on. Based on these results it can be concluded that during the pipefish reproduction period in the Wadden Sea, S. muticum beds provide efficient feeding grounds for E. aequoreus.

Since the growth of Sargassum muticum in the Wadden Sea is pseudo-perennial, the algal biomass decreases drastically during late summer and early fall, when lateral branches detach (Jephson & Gray 1977, Buschbaum et al. 2006). Therefore, S. muticum habitats are only temporarily available and do not support a resident fish fauna. While many pipefish species are considered to inhabit inshore habitats rather permanently (e.g. Kendrick & Hyndes 2003, Oliveira et al. 2007), Entelurus aequoreus can be regularly found offshore. Whether the pelagic mode represents a certain stage in the life cycle of snake pipefish or whether the oceanic forms of E. aequoreus are even taxonomically different from the inshore form is unclear (see Kloppmann & Ulleweit 2007 for details). Higher numbers of snake pipefish larvae in offshore plankton and of adult specimens in fish surveys might be a result of North Sea currents influencing the distribution of pipefish and their larvae, originating from inshore habitats. Active, seasonal inshore–offshore migrations are also possible, as has been documented for other synagnostid species, such as the northern pipefish Syngnathus fuscus, which leaves estuaries and moves offshore during winter (Lazzari & Able 1990).

Kirby et al. (2006) and Lindley et al. (2006) attribute the sudden numerical increase of Entelurus aequoreus in the northeast Atlantic to a warming sea as a result of climate change, which is beneficial for reproduction and larval survival. Environmental factors such as changing temperatures or the overexploitation of food competitors probably affect stocks of pipefish. However, those factors might not explain the sudden increase in stock sizes. The present study does not provide an exclusive reason for the increase of snake pipefish in the northeast Atlantic, but, in our opinion, the introduction of Sargassum muticum is a key factor for the recovery of E. aequoreus in the Wadden Sea. However, population dynamics and distribution patterns could not be demonstrated on a Wadden Sea scale in the present study, and we can only suggest that the settlement of pipefishes on transplanted S. muticum thalli occurred by passing pelagic specimens. However, since snake pipefish have been considered a red list species in the Wadden Sea (Berg et al. 1996), its sudden density and inshore aggregation in Sargassum habitats indicates a significant ecological function of S. muticum for these fish. Since S. muticum stocks are increasing in European waters (e.g. Critchley et al. 1987, Karlsson & Loo 1999, Staehr et al. 2000), a subject of further research should be whether these stocks could potentially trigger the high abundances of snake pipefish currently found in the northeast Atlantic Ocean.

That the complex structure of Sargassum muticum provides a significant shelter from predation can only be assumed, since this was not investigated during the present study. However, in our experience, specimens of Entelurus aequoreus were difficult to spot within the algal canopy, since they mimic S. muticum branches in colour and form. That different pipefish species occupy certain macrophytes based on their ability to mimic morphology and colour was observed by Kendrick & Hyndes (2003) in Western Australia. With their brownish colour and brighter markings, the camouflage of the snake pipefish we found matched S. muticum more closely than the seagrass (Zostera marina) habitats that they are documented to have formerly inhabited in the Wadden Sea area. Specimens recently illustrated or described (e.g. Froese & Pauly 2007) show a colouration similar to fish found during the present study and therefore are well camouflaged within S. muticum. We were not able to determine whether S. muticum habitats promote E. aequoreus densities more than seagrass habitats by offering a substrate that provides better camouflage, or whether snake pipefish simply adapt their colour to a changing habitat as other syngnathids do. However, this information is considered important to evaluate whether the introduction of S. muticum to the Wadden Sea leads to a restoration of snake pipefish stocks or whether it rather leads to an overpopulation that might negatively affect ecosystem functioning. Since historical data on pipefish abundance before the decline of subtidal seagrass beds are not available, it is difficult to evaluate whether the present increase of pipefish stocks might exceed the carrying capacity of the ecosystem and negatively influence other biota via the food web. Examples of such negative influences have already been reported by Harris et al. (2007), who observed that E. aequoreus increasingly became part of the diet of seabirds in the northeast Atlantic, negatively affecting their breeding success because chicks could not swallow snake pipefish and a high number of juvenile birds choked.
Beside snake pipefish, the sea stickleback Spinachias spinachia and the broad-nose pipefish Syngnathus typhle have been considered to be threatened in the Wadden Sea due to habitat loss (Berg et al. 1996). During the relatively short investigation period, 2 sea sticklebacks were observed within the transplanted Sargassum muticum thalli. Although the observation of 2 individuals is not enough to conclude that the alga affects the stock of S. spinachia in the Wadden Sea, it might indicate that a North Sea population of S. spinachia is still present in spite of the loss of Zostera marina habitats. In contrast to the snake pipefish and the sea stickleback, the broad-nose pipefish Syngnathus typhle is probably still absent in the northern Wadden Sea since the disappearance of subtidal seagrass (Polte 2004). Since S. typhle occurs in relative proximity—about 300 km northward, in the Danish Limfjord—the species’ geographical range does potentially allow a re-colonization of the Wadden Sea. Since reports of S. typhle to our knowledge are limited to seagrass habitats (e.g. Vincent et al. 1995, Riccato et al. 2003, Vizzini & Mazzola 2004, Oliveira et al. 2007), this species might rely on seagrass habitats and not take advantage of alternative habitats provided by Sargassum spp.

The introduction of non-indigenous species to all varieties of ecosystems is considered to be a major threat to global biodiversity (e.g. Steneck & Carlton 2001). However, depending on the capacity of ecological niches in the receptor system, it is also possible that introduced, habitat-forming organisms may promote the diversity of native communities instead of harming them. Buschbaum et al. (2006) found 60 species of epibionts associated with Sargassum muticum in the Wadden Sea, and a high number of them were originally rare in the area. However, there is also evidence of negative effects, e.g. on native algal assemblages caused by the introduction of S. muticum to other ecosystems. Britton-Simmons (2004), for example, showed that S. muticum introduced to the Pacific coast of the northern USA out-competed native macroalgae, and thus negatively affected the plant–grazer regime by limiting food availability to herbivores.

Thus, we conclude that the effects of non-indigenous, habitat-forming species such as Sargassum muticum may differ in distinct coastal systems. Although alteration of ecosystems by introduced species should never be promoted, consequences of introductions cannot be generalized but could be—and should be—investigated in relationship to the unique characteristics of the receptor system.

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