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# Adapted for invasion? Comparing attachment, drag and dislodgment of native and nonindigenous hull fouling species

Cathryn Clarke Murray · Thomas W. Therriault · Patrick T. Martone

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**Abstract** Invasive species possess unique traits that allow them to navigate the invasion process in order to establish and spread in new habitats. Successful hull fouling invaders must resist both physical and physiological stressors associated with their voyage. We characterised attachment strength and drag coefficient of common fouling species in order to estimate the velocity required to dislodge them from boat hulls. We hypothesized nonindigenous fouling species would possess biomechanical properties that enable them to remain attached to hulls more successfully than similar native species. Indeed, the well-known invasive ascidian *Styela clava* had both high attachment strength and low drag coefficient and its dislodgment velocity was well above that of fast moving vessels. In contrast, the native congener *Styela gibbsii* had low attachment strength and higher drag coefficient. Colonial invasive species employed a different hitchhiking strategy;

despite their low attachment strengths, *Botrylloides violaceus* and *Didemnum vexillum* had low drag coefficients allowing them to be transported on slower-moving vessels, such as sailboats and barges. The biomechanical adaptations of invasive species show promise in predicting future invaders and informing vector management strategies at the first node in the invasion process: transport by the vector.

**Keywords** Hull fouling · Biomechanics · Dislodgment velocity · Attachment strength · Drag coefficient

## Introduction

Theories abound as to which traits make certain nonindigenous species become invasive. There is evidence that adaptation to disturbance (Altman and Whitlatch 2007; Hobbs 1992), wide environmental tolerances (Marchetti et al. 2004; McMahon 1996), rapid growth and/or high reproductive capabilities (Marchetti et al. 2004; McMahon 2002) assist nonindigenous species in establishment and subsequent spread (Kolar and Lodge 2001; Lodge 1993). These adaptations may have evolved in response to processes in their native range or may have been rapidly selected for within their newly invaded range. For example, in Australia cane toads at the leading edge of the invasion front have longer legs than those in older established populations, conferring a faster rate of spread

C. Clarke Murray (✉)  
Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, BC, Canada  
e-mail: cclarke@eos.ubc.ca

T. W. Therriault  
Pacific Biological Station, Fisheries and Oceans  
Canada, Nanaimo, BC, Canada

P. T. Martone  
Botany Department and Biodiversity Research Centre,  
University of British Columbia, Vancouver, BC, Canada

(Phillips et al. 2006). Thus, adaptations of invasive species are not only of ecological interest but may inform conservation and management decisions.

Researchers have used physiological tolerances to predict invasion and range expansion of invasive species, examining temperature, altitude, depth, salinity, vegetation cover and many other variables (Dark 2004; Epelbaum et al. 2009; Herborg et al. 2008; Johnson et al. 2001). However, these types of analyses are only useful for explaining potential patterns of establishment, the final stage of invasion. The first step in the invasion process is uptake by a human-mediated vector either intentionally or accidentally (e.g. settling on the hull of a freighter or being drawn into ballast water tanks) (Lockwood et al. 2005). Successful invaders must then survive the journey to the new location outside their native range. Previous modelling efforts to predict the potential distribution of an invader largely have not considered this uptake and transport stage explicitly.

Hull fouling is one of the earliest documented marine vectors. Wood-boring invaders, such as the shipworm bivalve *Teredo navalis*, have been travelling the world's seas as long as wooden ships (Hoppe 2002). Moreover, hull fouling invaders have evolved in concert with developments in the shipping industry. For example, antifouling paints and the subsequent ban of Tributyl Tin (TBT) have shaped the frequency and type of hull fouling invaders (Dafforn et al. 2008; Evans et al. 2000; Piola et al. 2009). The increase in size and speed of international ships has increased the surface area available for colonization, decreased transit time between ports, and facilitated invasions (Carlton 1996; Levine and D'Antonio 2003). Some examples of long distance hull fouling invaders include the black-striped mussel (*Mytilopsis sabei*) in Australia (Field 1999), the barnacle *Chthamalus proteus* in Hawaii (Southward et al. 1998), and the kelp *Undaria pinnatifida* in New Zealand (Floerl and Inglis 2005). In addition, there are many examples of secondary or regional spread attributed to recreational boating activities, including freshwater zebra mussels (*Dreissena polymorpha*) (Johnson et al. 2001) and the ascidian *Styela clava* in marine waters (Floerl and Inglis 2005; Locke et al. 2007). However, only a few studies have explicitly tested the ability of nonindigenous species to endure the voyage. For example, to evaluate the risk of overland transport by trailered boats, studies showed that zebra mussels can remain

viable out of water for up to four days (McMahon 1996) while the ascidian *Styela clava* tolerated 48 h of air exposure with low mortality rates (Darbyson et al. 2009).

Underwater hulls of boats are complex three-dimensional surfaces. Niche or non-hull areas, including the vents, propeller, and rudder, typically experience different flow regimes compared to smooth hull surfaces. Those surfaces in the lee of the keel, for example, experience reduced flow velocities while those protruding into flow may experience higher velocities. Fouling levels on recreational boats can be much higher in niche areas, not only due to differences in paint application or effectiveness but also due to localized reduction of velocity in these areas (Clarke Murray et al. 2011; Davidson et al. 2010). Similarly, fouling panels attached to commercial ships have demonstrated differences in community composition among different areas of vessels (Coutts et al. 2007). These results suggest that hydrodynamics may be an important selective pressure for hull fouling species.

Hull fouling transport may be another example of a selection regime modification (Byers 2002) where hydrodynamic conditions experienced *en route* are substantially different than any experienced under natural conditions, potentially selecting for nonindigenous species over native ones. Thus, it is probable that hull fouling invasive species have adaptations that provide a competitive advantage and allow them to remain attached to boat hulls long enough to reach new habitats. These adaptations may include superior attachment properties and/or drag reduction strategies. Barnacles and mussels are common hull fouling organisms whose spread has been linked to shipping activities worldwide (Kado 2003; Laird and Griffiths 2008; Pilsbry 1916; Schwindt 2007). For example, the Atlantic barnacle *Chthamalus proteus* was found fouling ships above the water line in Hawaii (Southward et al. 1998) and the introduction of *Eliminius modestus* to Ireland was traced to hull fouling on transport ships during World War II (Lawson et al. 2004). Barnacles have a broad base that cements to the substrate, likely conferring superior biomechanical properties to remain attached to boat hulls. In contrast, mussels attach using flexible byssal threads, an extracellular, collagen-like material and attachment strength is related to the number of byssal threads and varies by season, wave exposure, and bed location (Bell and Gosline 1997; Carrington 2002; Hunt and

Scheibling 2001; Witman and Suchanek 1984). Previous studies have suggested that water velocity is a highly selective force for mussel species (Schneider et al. 2005) and in Europe the abundance of *M. galloprovincialis* is positively related to wave exposure (Gosling and Wilkins 1981; Hilbish et al. 2002; Skibinski and Roderick 1991). Many mussel invasions have been linked to recreational boating as a vector including zebra mussels in the Great Lakes region of North America (Bossenbroek et al. 2007; Padilla et al. 1996) and black-striped mussels in Darwin, Australia (Field 1999).

Beyond barnacles and mussels, little is known about attachment and drag of other fouling species. A previous study in British Columbia (BC), Canada documented a number of fouling species common to the submerged surfaces of recreational boats (Clarke Murray et al. 2011). Differing morphological types may affect their ability to endure hydrodynamic conditions of traveling boats and their ability to spread with this vector. Encrusting nonindigenous species such as *Botryllus schlosseri*, *Botrylloides violaceus*, *Didemnum vexillum* and *Halichondria bowerbanki* form mat-like colonies that grow horizontally across surfaces suggesting they may be less susceptible to drag and dislodgment. Solitary ascidian species, such as *Corella inflata*, *Styela gibbsii* and *Styela clava* vary in body shape and size. The stalk of *S. clava*, a nonindigenous species in BC, can grow to 15 cm, whereas *S. gibbsii* is attached broadly at the base of the body and only grows to 6 cm. *C. inflata* has a broad base, is roughly rectangular in shape and compressed laterally, reaching 5 cm in length. Although all three species are common on floating docks and pilings of harbours and small craft marinas, only *C. inflata* and *S. clava* were observed attached to recreational boats (CCM unpublished data) suggesting that these species may differ in their ability to withstand the hydrodynamic conditions of hull fouling or tolerance for toxic antifouling paints. Therefore, nonindigenous species such as *S. clava* may be better adapted to the hydrodynamic environment experienced while attached to traveling boats, allowing it to invade new environments.

We hypothesize that hull fouling invaders possess traits that allow them to settle and remain attached to vessels until suitable habitat is reached. Solitary species, may then release reproductive gametes which settle on the same (boat hull) or different substrates

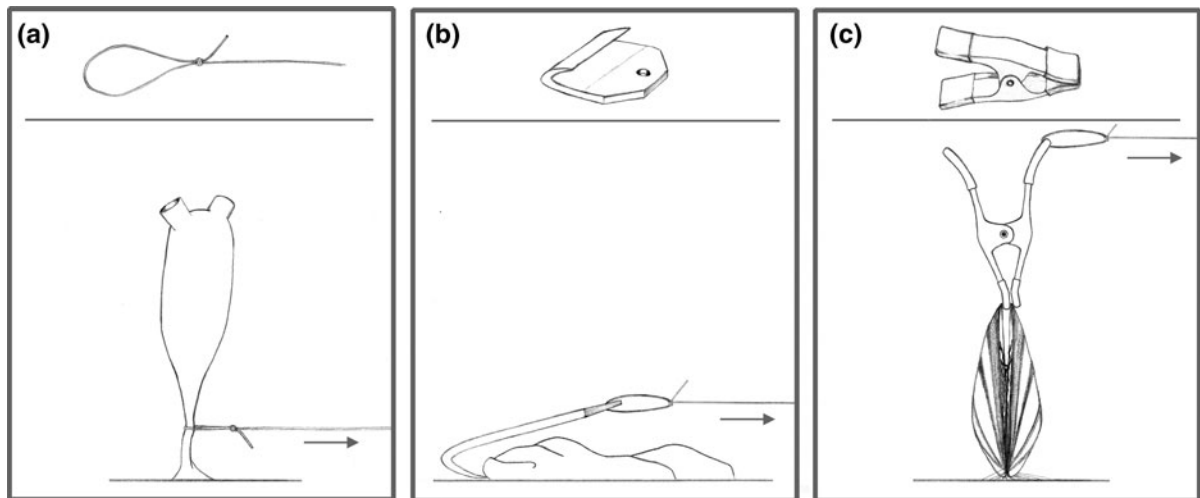
(other boats, floating docks or pilings) in the new location while colonial species additionally may fragment and re-grow in the new habitat. Mechanical properties that allow fouling species to remain attached to marine travelling boats have not been quantified previously and may provide insight into vectors of introduction as well as patterns of invasion. In this study we investigate the biomechanical properties of eight common fouling species, both native and nonindigenous. We quantify dislodgment strengths and drag forces in order to estimate the velocity at which species will be dislodged from boat hulls, allowing us to compare to possible vectors of introduction and spread.

## Methods

### Attachment strength

Recording spring scales were used to measure the force required to dislodge or break common fouling species (attachment strength,  $F_{\text{dislodge}}$ ) measured in Newtons of force (N). We measured the attachment strength of the following species: native ascidians *S. gibbsii* and *C. inflata*, barnacle *B. glandula* and nonindigenous ascidians *S. clava*, *B. violaceus* and *D. vexillum*, sponge *Halichondria bowerbanki*, and the cryptogenic mussel *Mytilus* species complex. Species of *Mytilus* were grouped because the nonindigenous species *Mytilus galloprovincialis* and *Mytilus edulis* have hybridized with the native *Mytilus trossulus* making them indistinguishable without the aid of genetic testing. Measurements were taken from floating docks and pilings at four marinas: Institute of Ocean Sciences, Royal Vancouver Yacht Club Jericho, Royal Victoria Yacht Club and Thetis Island Marina in British Columbia, Canada. Not all species were present at all marina locations. The spring scale was attached to individuals by a monofilament noose, rubber clip or recurved scraper and then pulled parallel to the surface in the direction of water flow (Fig. 1). Effort was made to pull the spring scale repetitively in the same manner for all individuals and the same attachment device was used for all individuals tested within each species. Species identity, height, attachment area, failure location (stalk, fragment, byssus, shell, etc.), and substrate type (wooden dock, piling, or cement) were recorded for all individuals. Height and





**Fig. 1** Illustrations of attachment devices used with recording spring scale to measure force of attachment with examples of their use: **a** monofilament noose on solitary ascidian, **b** recurved

scraper on colonial ascidian, and **c** rubber clip on mussel. Arrows indicate direction of force

attachment area were measured used calipers. The effect of species and marina location on attachment strength was tested using General Linear Model ANOVA (Attachment strength = Intercept + Species + Marina + Error). Only *Mytilus* was tested on more than one substrate type (floating wooden dock and natural rock) so the effect of substrate type on attachment strength of this species was tested using non-parametric Mann–Whitney *U*-test because the equality of variance assumption was violated. The relationship between attachment strength and height was tested using Pearson correlations.

To investigate the importance of attachment strength to presence/absence of species we compared the mean measured attachment strength of each species to their field occurrence from a previous dive survey of hull fouling communities of 491 recreational boats (for full details of the survey see Clarke Murray et al. 2011). We would predict that if attachment strength was a limiting factor in transport by this vector there would be a strong correlation with field occurrence on small boats, although the boat data represented both active and inactive boats which could affect the correlation. From the survey data, the percentage of boats with each nonindigenous species present was recorded and this data used in Pearson correlation analyses with attachment strength. All statistical analyses were performed using SPSS with  $\alpha$  level set at 0.05.

## Drag force

Individuals of five species (*B. violaceus*, *C. inflata*, *D. vexillum*, *S. gibbsii*, and *S. clava*) were collected from the two field sites and further tested in a custom high-speed recirculating flume (Ecological Mechanics, Rochester, NY, USA). Individuals of solitary species were suspended from a quarter-inch screw at their natural attachment site using gel superglue. The test screw was inserted into a force transducer (FORT5000, World Precision Instruments, Sarasota, FL, USA) and drag force was recorded at nine velocities (0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8 and 2.0 m/s). For comparison, maximum sailboat velocity is approximately 3.6 m/s and maximum powerboat velocity is approximately 20.5 m/s. Flow was turbulent at the velocities tested, as would likely be experienced under boat hulls. Colonial species were attached to circular compact discs (12 cm diameter) along the entire natural attachment area of the colony using gel superglue. Drag on colonial species was only measured at seven velocities due to their low drag profile and a comparable drag on the compact discs alone (0.2, 0.4, 0.6, 0.8, 1.0, 1.2 and 1.4 m/s). The baseline level of drag due to the experimental apparatus was determined using the test screw and disc without individuals attached. Height was recorded for each individual prior to testing. Digital photographs were taken of the specimen in the test chamber prior to

water flow, and Software program Image J (developed by Wayne Rasband, National Institutes of Health, Bethesda, MD, USA) used to calculate maximum planform area of each specimen from the photographs.

## Data analysis

Species in hull fouling communities are subjected to drag forces, which can be calculated from the following equation:

$$F_{\text{drag}} = 1/2 \rho U^2 A C_d \quad (1)$$

where  $F_{\text{drag}}$  is drag force,  $\rho$  is density of water,  $U$  is water velocity,  $A$  is maximum planform area, and  $C_d$  is drag coefficient. Note that  $A$  is maximum planform area (not projected area) and is therefore assumed to be invariant with water velocity. This assumption is standard practice in most hydrodynamic studies of flexible organisms, such as seaweeds, bypassing the difficulties of measuring area in turbulent flow and allowing drag coefficient to be the sole measure of flexible reconfiguration and reorientation (see Carrington 1990; Gaylord et al. 1994; Koehl 2000; Johnson 2001; Martone and Denny 2008a, b).

## Calculating drag coefficients

Drag coefficients were calculated by re-arranging Eq. 1 to yield:

$$C_d = \frac{2F_{\text{drag}}}{\rho U^2 A} \quad (2)$$

For each individual tested, drag coefficients were calculated over the entire range of velocities and the mean  $C_d$  was plotted against velocity to produce a characteristic  $C_d$ - $U$  curve for each species.

## Predicting dislodgment

Fouling organisms would be expected to dislodge when drag force ( $F_{\text{drag}}$ ) experienced equals dislodgment force ( $F_{\text{dislodge}}$ ). Dislodgment velocity was estimated by rearranging Eq. 1 such that:

$$U_{\text{dislodge}} = \sqrt{\frac{2F_{\text{dislodge}}}{\rho A C_d}} \quad (3)$$

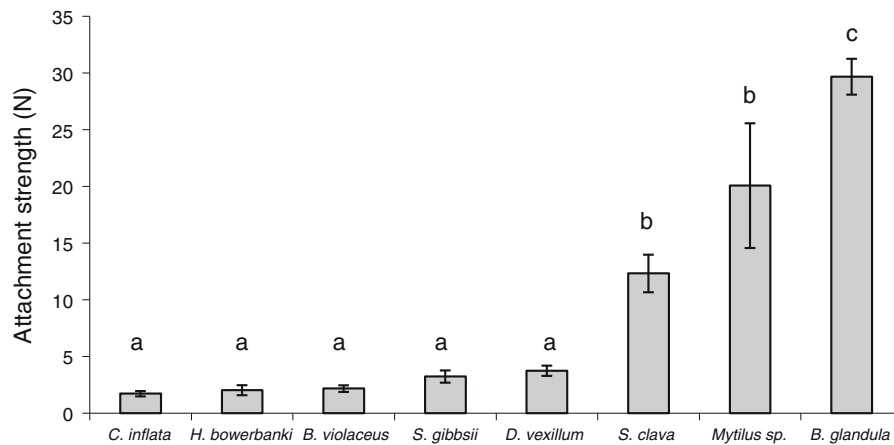
where  $A$  was the maximum planform area of each individual tested, species-specific drag coefficients

$C_d$  were calculated from Eq. 2. For three species, *S. gibbsii*, *D. vexillum*, and *B. violaceus*, drag coefficient remained constant across velocities so the grand mean drag coefficient was used to calculate dislodgment velocity. For *S. clava* and *C. inflata* drag coefficient decreased with velocity. To calculate dislodgment velocity for these species, we used the drag coefficient measured at the highest velocity tested (2.0 m/s), following the method of Bell (1999 Extrapolation model B) and the average dislodgment strength measured for the species. This yields a range of minimum dislodgment velocities that vary with size. To determine whether each species would be carried on marine vessels, the estimated minimum dislodgment velocity was compared to reported maximum velocities of recreational marine vessels (powerboat and sailboat). If the estimated dislodgment velocity was lower than the vessels' maximum velocity, we predicted that the species would be dislodged by that vessel.

## Results

### Attachment strength

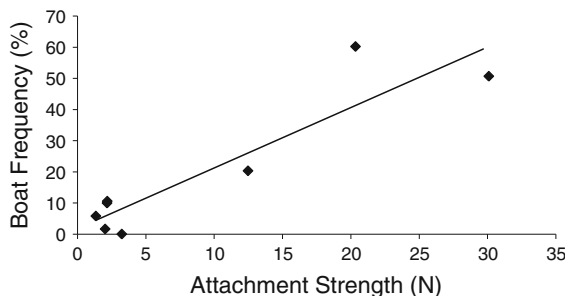
The most strongly attached fouling species were the solitary species *B. glandula*, *Mytilus* sp. and *S. clava* (Fig. 2). There were significant differences among species tested for attachment strength (GLM ANOVA:  $F = 14.061$ ,  $df = 5$ ,  $p < 0.001$ ). The weakest attachment force was that of the solitary ascidian *C. inflata*, colonial sponge *H. bowerbanki*, and colonial ascidian *B. violaceus*. Attachment of *B. glandula* was significantly stronger than all other species. Attachment strengths of *Mytilus* sp. and *S. clava* were less than *B. glandula* but greater than other species and not significantly different from each other (Tukey's HSD post hoc,  $p < 0.05$ ). The attachment of the nonindigenous ascidian *S. clava* was significantly stronger than the native solitary ascidians *C. inflata* and *S. gibbsii*. Marina location had no significant effect on attachment strength (GLM ANOVA: main effect  $F = 0.477$ ,  $df = 2$ ,  $p = 0.621$ ). Attachment strength of *Mytilus* spp. was significantly higher on wooden docks (Mean =  $25.86 \pm 1.743$  SE) than on rocks (Mean =  $11.96 \pm 0.906$  SE) (Mann-Whitney  $U$ -test:  $Z = -2.846$ ,  $p = 0.004$ ).



**Fig. 2** Attachment strength (N) for fouling species tested by recording spring scales. Letters denote statistically significant post hoc groupings (GLM ANOVA, Tukey's HSD post hoc test)

Species with highest measured attachment strength also were the most commonly observed in hull fouling communities of recreational boats (data from Clarke Murray et al. 2011). Attachment strength measured for each of the eight fouling species was strongly correlated to their incidence in boat hull fouling communities (Fig. 3, Pearson's  $r = 0.915$ ,  $p = 0.001$ ).

Location of breakage differed between colonial and solitary species (Table 1). Breakage occurred at the base or stalk for solitary species (*B. glandula*, *S. clava*, *S. gibbsii*, and *C. inflata*). In contrast, for colonial species (*D. vexillum*, *B. violaceus* and *H. bowerbanki*), complete dislodgment was rare and most colonies simply fragmented under experimental conditions (i.e. part of the colony broke off but some always remained attached to the substrate). Attachment



**Fig. 3** Correlation between attachment strength (N) of each fouling species and their corresponding frequency in boat hull fouling communities [boat frequency data from (Clarke Murray et al. 2011)] (Pearson's correlation  $r = 0.915$ ,  $p = 0.001$ )

strength increased with individual height only for *S. clava* (Pearson correlation  $F = 20.798$ ,  $p < 0.001$ ,  $R^2 = 0.510$ ) and *Mytilus sp.* (Pearson correlation  $F = 37.624$ ,  $p < 0.001$ ,  $R^2 = 0.35$ ).

#### Drag force

Drag coefficients of solitary species *C. inflata* and *S. clava* decreased as a function of velocity (Fig. 4a). These two species demonstrated the ability to reconfigure at increasing velocities, *S. clava* bends at its flexible stalk (Fig. 5) while *C. inflata* reconfigured to a lesser extent by bending its entire body and thus reducing its area projected into the flow. The other solitary ascidian, *S. gibbsii*, and colonial species *D. vexillum* and *B. violaceus* did not reconfigure in flow and their drag coefficients varied little with increasing velocities (Fig. 4). Mean drag coefficients were used in further calculations for these three species (*S. gibbsii* =  $0.156 \pm 0.005$ , *D. vexillum* =  $0.016 \pm 0.003$ , *B. violaceus* =  $0.093 \pm 0.028$ ). Variability in drag coefficient was higher for colonial species than solitary species tested (Fig. 4).

#### Dislodgment velocity

Dislodgment velocity was highest for *S. clava* ( $27.30 \pm 4.04$  m/s), followed by *C. inflata* ( $16.1 \pm 1.0$  m/s), and *S. gibbsii* ( $15.4 \pm 1.7$  m/s) (Fig. 6). Most individuals of *S. clava* had dislodgment velocities higher than powerboats and sailboats. In contrast, *S. gibbsii* and *C. inflata* had dislodgment velocities



**Table 1** Dislodgment location (base, byssus, stalk, attachment disc or fragment) for solitary and colonial species tested by recording spring scales (%)

		Dislodgment location (%)				
Type	Species	Base	Byssal threads	Stalk	Attachment disc	Shell
Solitary	<i>B. glandula</i> (n = 30)	100	NA	NA	NA	0
	<i>C. inflata</i> (n = 14)	100	NA	NA	NA	NA
	<i>Mytilus</i> sp. (n = 47)	NA	100	NA	NA	0
	<i>S. clava</i> (n = 28)	75	NA	17.9	7.1	NA
	<i>S. gibbsii</i> (n = 21)	87.5	NA	12.5	NA	NA
			Dislodgment location (%)			
Type	Species	Fragment			Colony dislodgement	
Colonial	<i>B. violaceus</i> (n = 23)	100			0	
	<i>H. bowerbanki</i> (n = 7)	100			0	
	<i>D. vexillum</i> (n = 20)	100			0	

For solitary species, “Base” is the bottom of the individual in contact with the surface, “Byssal threads” refers to *Mytilus* only, “Stalk” refers only to species of *Stryela* with a stalk of varying length, “Attachment disc” refers to *S. clava* only and is a large disc at the base of the stalk which is attached to the substrate. For colonial species, dislodgment was either “Fragment” where some part of the colony broke and some remained attached to the substrate or “Colony dislodgement” which occurred when the entire colony peeled from the substrate intact. “NA” means that dislodgment location category was not applicable to that species

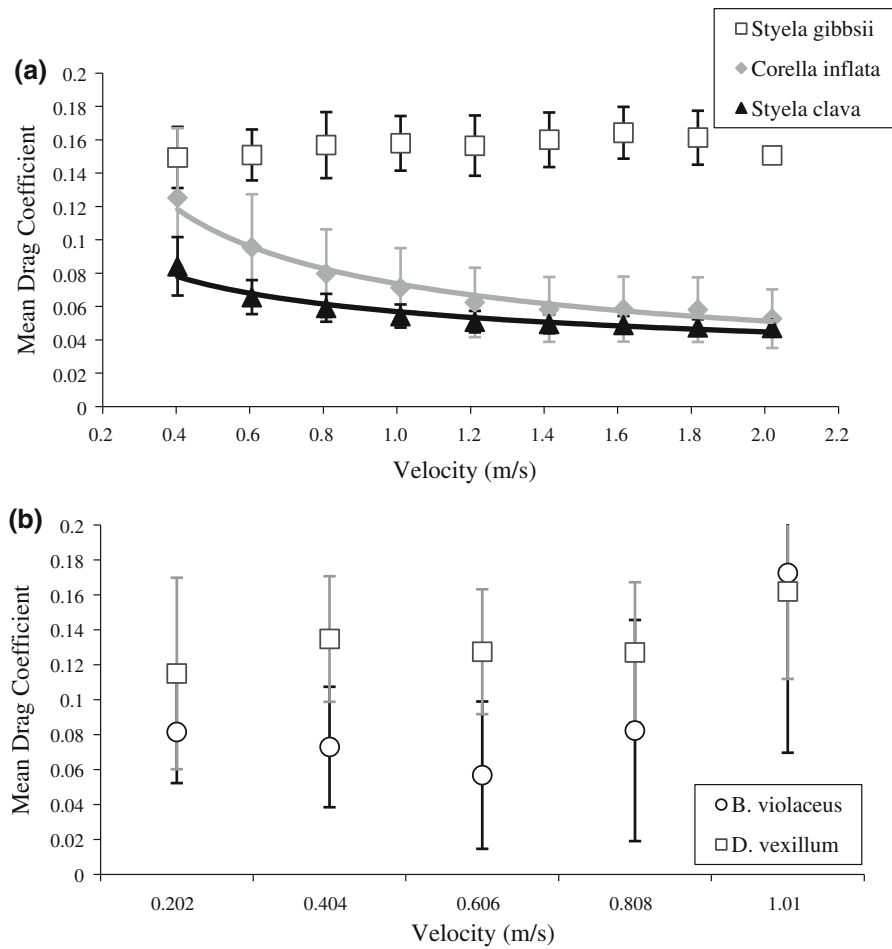
slower than powerboats but higher than sailboats (Fig. 6). The dislodgment velocities of colonial species *D. vexillum* and *B. violaceus* ( $9.7 \pm 1.7$  and  $6.8 \pm 1.1$  m/s, respectively) were much slower than powerboat velocity but still faster than maximum sailboat velocity.

## Discussion

Our results show that three common hull fouling invaders (*S. clava*, *D. vexillum* and *B. violaceus*) have the ability to remain attached to marine vessels. Although all five species tested are common fouling species and could be carried on sailing vessels, it appears that only *S. clava* would be regularly carried on faster-moving power boats. *S. clava* was the most common nonindigenous species encountered on the hulls of both sail and powerboats in a previous study (Clarke Murray et al. 2011). This species was likely transported globally on naval ships in conjunction with the Korean War (Clarke and Therriault 2007), and the timing of first introduction to California (1933) suggests that the original introduction vector may have been ship hull fouling (Abbott and Johnson 1972). Further, its secondary spread has been linked to recreational boating activities on the east and west

coasts of North America (Clarke Murray et al. 2011; Darbyson et al. 2009; Lambert and Lambert 1998). Here we show that this worldwide invader has a dislodgment velocity much greater than that of all vessel types—a consequence of its flexible reconfiguration, low drag coefficient, and high attachment strength. Flexible reconfiguration is a common strategy of many sessile marine organisms to reduce drag forces (Boller and Carrington 2006; Denny 1994; Koehl 1984; Vogel 1984). In sum, our results support the efficacy of boat-hull transport for this organism.

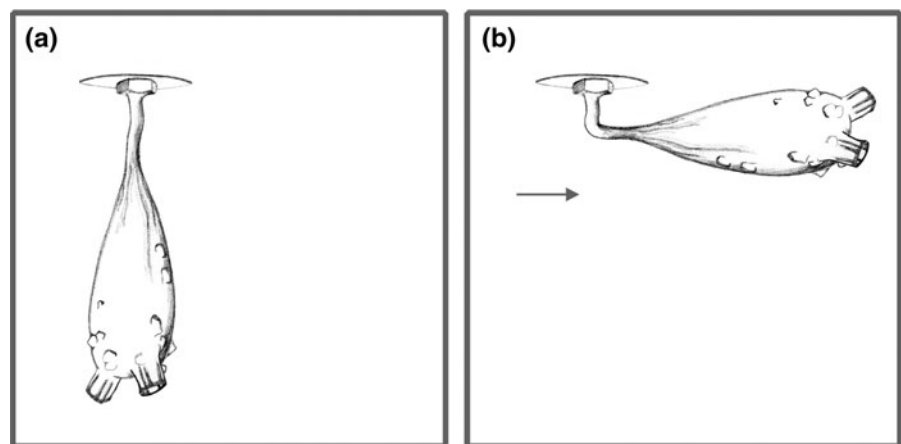
Despite their low attachment strength, the colonial tunicates tested (*B. violaceus* and *D. vexillum*) could be dispersed on slower-moving vessels such as sailboats and barges. Their low profile reduces drag, projecting a much smaller perpendicular area to water flow. In laboratory tests of a *Botrylloides* species from San Francisco, Edlund and Koehl (1998) found that the tissue strength of *Botrylloides* colonies was much stronger than their attachment to the substrate. To the contrary, our results suggest that colonies of *B. violaceus* and *D. vexillum* were more likely to fragment than to peel completely from the substrate. Such fragmentation may be an important survival strategy, reducing the probability that complete dislodgment occurs. Fragments of botryllid ascidians have the ability to reattach (Worcester 1994) and this

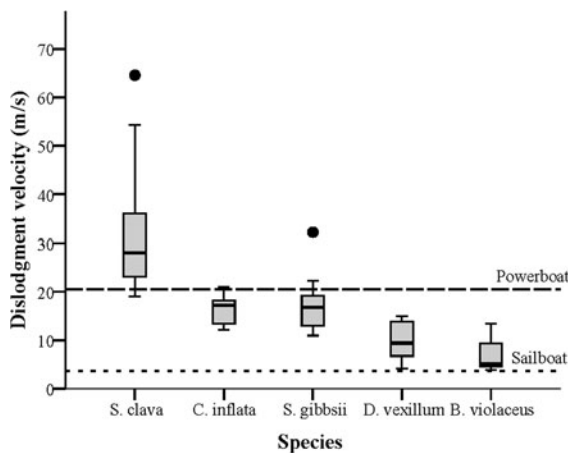


**Fig. 4** Drag coefficient (mean  $\pm$  SE) by velocity for **a** solitary and **b** colonial species. Regression curves: *S. clava*  $y = 0.057x^{-0.3454}$ ,  $R^2 = 0.9438$  and *C. inflata*  $y = 0.0737x^{-0.5212}$ ,  $R^2 = 0.9702$ .

Sample sizes *S. gibbsii*  $N = 12$ , *C. inflata*  $N = 9$ , *S. clava*  $N = 12$ , *B. violaceus*  $N = 9$ , *D. vexillum*  $N = 12$

**Fig. 5** Illustration of reconfiguration of *Styela clava* in the flume **a** at rest and **b** in flow. Arrow indicates direction of water flow and length represents scale, 2 cm





**Fig. 6** Boxplot of estimated dislodgment velocity by observed sizes for each species. Dashed reference lines indicate top speed for sailboat (3.6 m/s) and powerboat (20.5 m/s). Any individuals below the line should be dislodged. Black dots indicate predictions outside the 95% confidence intervals

may be an important part of the invasion process for these species. Rafting on broken eelgrass blades and subsequent reattachment has been shown to be a more efficient dispersal strategy over large distances than larval swimming (Worcester 1994). Such “programmed breakage” also has been observed in wave-battered corals and algae where fragments frequently break and regrow (Anderson et al. 2006; Highsmith 1982). Additionally, these ascidian species produce three-dimensional growth forms (lobes, strings, etc.) which could experience higher drag and increased risk of fragment dislodgment. Further testing is required to determine if there are differences in attachment strength among these vertical growth forms compared to horizontal colonies. Dislodgment of three-dimensional growths may be an effective dispersal strategy, such that the colony remains attached to the boat but pieces break off to establish new colonies in visited harbours.

The native solitary ascidians *S. gibbsii* and *C. inflata* had low attachment strength but experienced comparable drag to that of the larger *S. clava* despite their small size likely because they were unable to reconfigure in flow. On average, the dislodgment velocity for these species was slower than powerboat velocity, suggesting they could only be transported on slower-moving boats. However, dislodgment velocity is only one factor to consider in invasion dynamics:

settlement preferences, larval behaviours, hydrodynamics, and early mortality dynamics may limit the presence of fouling species on boats (Koehl 2007; Pawlik 1992) thereby lowering their entrainment potential in the vector. Niche areas often harbour disproportionately higher amounts of fouling species than smooth hull surfaces likely because of the reduction in flow and an absence of antifouling paint application (Coutts et al. 2007; Clarke Murray et al. 2011; Davidson et al. 2011). Thus, estimated dislodgment velocity may underestimate the probability of transport for individuals protected by niche areas.

Two species tested in the current study, *S. gibbsii* and *D. vexillum* were predicted to be transported on slower-moving vessels but were not observed in the fouling communities of sailboat or powerboats despite being present on nearby floating structures (Clarke Murray et al. 2011). Therefore, displacement velocity loses predictive power if organisms do not settle on vessels as a result of reproductive timing or settlement preferences. However, settlement preferences also may promote the transport of invasive species on marine vessels. For example, the invasive bryozoan *Watersipora subtorquata* is a fouling species with high tolerance to copper antifouling compounds applied to commercial and recreational boats (Floerl et al. 2004) and even prefers to settle on treated areas (Dafforn et al. 2008; Piola and Johnston 2009). It is unknown if invasive ascidians have similar adaptations to antifouling chemicals as these properties have not yet been tested.

Little information exists about the attachment of ascidians. The colonial ascidians *Perophora viridis* and *Amaroucium constellatum* attach initially using a viscous adhesive secretion laid down by the papilla (Grave and McCosh 1923 IN Lane 1973). The structure of the attachment disc of *S. clava* appears very different from the fibrous attachment of *S. gibbsii*; *S. clava* has a flat, disc-like attachment compared to *S. gibbsii* that had a bumpy, uneven attachment site (CCM pers obs). Of the solitary ascidians, only *S. clava* exhibited stronger attachment strength with height. There was no corresponding increase in attachment site size suggesting that this species either deposits more adhesive or lays down stronger adhesive as it grows.

Attachment strength was measured for *Mytilus* sp. on a subset of typical fouling substrate types: floating wooden docks and natural rock. The presence of artificial structures has been shown to promote

dominance of invasive species (Dafforn et al. 2009; Tyrell and Byers 2007) and substrate type was important in determining attachment strength for the cryptogenic *Mytilus* sp. complex here. Unfortunately, the other species studied were not found on each of the three substrates but it is highly likely to be an important variable for other species as well. Further research is required to investigate the role of substrate in attachment of other hull fouling species. This is especially critical in addressing the attachment upon marine vessels protected by antifouling paints, not tested in the current work. While traditional antifouling paints employ toxic biocides that prevent invertebrate larval settlement, some types of antifouling paint are specifically designed to prevent species from remaining attached while a vessel is moving (Piola et al. 2009; Schultz et al. 1999). These ablative or fouling-release paints slough off the top layer with movement removing the associated fouling organisms.

Extrapolating drag forces from laboratory flume conditions (2 m/s) to environmentally relevant water velocities or boat speeds (20 m/s) may be problematic because of uncertainty in drag coefficient (e.g. Bell 1999; Denny and Gaylord 2002; Gaylord et al. 1994). The colonial species tested had higher variability in drag coefficient than solitary species but this is likely a result of the higher drag of the disc apparatus used to suspend individual colonies within the flume. Mortality predictions based on dislodgment models often have high degrees of associated error (Denny 1995; Mach et al. 2007 but see Martone and Denny 2008a). Recent studies show that data collected at higher speeds (up to 4 m/s) improves drag predictions for some hydrodynamically-stressed macroalgal species, but not for others (PTM, unpublished data). In this study, we acknowledge this uncertainty and have chosen to be conservative in our drag coefficient extrapolation for *S. clava* and *C. inflata*, assuming no decrease in  $C_d$  with increasing velocity above 2 m/s (see Bell 1999, Extrapolation Model B). Thus, dislodgment velocities calculated here represent minimum estimates for these species. If  $C_d$  continues to decrease with increasing velocity for these species, predicted dislodgment velocities would increase, suggesting that these species may be able to resist even faster boat velocities before being dislodged.

An additional source of uncertainty in predicting dislodgment is the location of individuals within “beds” or dense fouling communities that may be

primarily subjected to lift forces, rather than drag forces. For mussels, Bell and Gosline (1996) predicted that attachment measured parallel to the substratum is 53–57% of that measured perpendicular to it. The angle of lift and drag forces experienced by the organism would vary with location on the boat, community composition, and fouling density as well as solitary versus encrusting growth forms and these relationships have not been quantified for other fouling species. The development of complex fouling communities on vessels also can drastically reduce the drag experienced by individual members within a community, as previously shown for dense seaweed communities (Johnson 2001). In this manner, gregarious settlement, as occurs in barnacles and other marine organisms, can lead to sheltering (Schultz et al. 1999). Complex communities provide microhabitats for smaller sessile and mobile species, allowing them to be transported with travelling vessels, as has been hypothesized for the invasive amphipod *Caprella mutica* (Frey et al. 2009). Therefore, estimating dislodgment velocity based on solitary individuals may lead to an underestimation of the probability of transport to new habitats.

Single force application, such as the pull-to-break measure of attachment strength used here, may also lead to an underestimation of dislodgment. Previous authors found low probabilities of breakage compared to field observations (Gaylord et al. 1994; Gaylord 2000; Johnson and Koehl 1994; Kitzes and Denny 2005; Utter and Denny 1996 but see Martone and Denny 2008b). Two additional mechanical properties may affect dislodgment over time: fatigue fracture and creep (Vogel 2003). Fatigue fracture, or repeated loading of smaller stresses, has been shown to be important for wave-swept organisms such as intertidal macroalgae (Mach et al. 2007, 2011). Fatigue fracture is not accounted for in the current dislodgment model and has not been well characterized in general (Koehl 1984; Mach et al. 2007). Creep, on the other hand, occurs when soft-bodied organisms slowly stretch or deform in response to constant force application (Koehl 1984). This has been well-studied in anemone mesogleal tissues and the same likely applies to solitary ascidians that also have hydrostatic skeletons. With constant force application, anemone tissues have been shown to reversibly deform and the degree of deformation depends on the time scale of force application (Koehl 1984, 1999). Attachment strength

measured here is more representative of instantaneous forces, such as initial acceleration of a boat. However, creep experienced by organisms attached to a cruising boat has not been characterized but may lead to dislodgment at smaller forces during long slow boat voyages.

The three solitary species tested have the ability to retract their siphons when disturbed and they demonstrated this behaviour during experiments in the recirculating flume. This suggests that their ability to filter water and feed may be restricted when water velocity increases. New invasions can only be seeded by individuals that survive the voyage and reproduce in the new environment. Therefore, although they have the physical ability to remain attached, these species may not survive trans-oceanic voyages to invade new areas if filter-feeding time is critically limited. Similarly, environmental conditions within ballast tanks have been found to limit the survival of potential ballast water invaders (Flagella et al. 2007; Gollasch et al. 2000). Further study is required to determine effect of voyage duration, speed, and surface chemistry (such as anti-fouling paint) on survivorship of hull fouling invaders.

In conclusion, the nonindigenous species tested here demonstrated adaptations that allow them to remain attached to travelling vessels. Two successful strategies were observed for nonindigenous species, solitary species possessed low drag coefficients as a result of reconfiguration combined with high attachment strength. Colonial, asexually reproducing nonindigenous species had extremely low drag profiles coupled with low attachment strength which may contribute to fragmentation and dispersal. We demonstrated that the nonindigenous ascidians *S. clava*, *D. vexillum* and *B. violaceus* have the biomechanical ability to travel with marine vessels, suggesting that these species can be introduced and spread via hull fouling. Biomechanical properties, such as high attachment strength and reconfiguration in flow may contribute to the ability of hull fouling nonindigenous species to invade new habitats throughout the world. As little is known about these species in their native habitats, we can only speculate that high attachment strength and the ability to reconfigure evolved in response to high flow conditions. These adaptations may have been further selected for through the mechanism of selection regime modification of the hull fouling vector (Byers 2002). Only those individuals with the mechanical ability to withstand the hydrodynamic conditions of the

human-mediated voyage would survive to invade the new region. Biomechanical parameters could be used to assess potential invaders for the ability to travel via hull fouling vectors and allow researchers to model species movements more effectively. In addition, this type of research can assist in the development of antifouling technologies and inform vector management in order to reduce the introduction and spread of invasive species.

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