

Migration of large-scale subaqueous bedforms measured with seagrasses (*Cymodocea nodosa*) as tracers

Abstract—The vertical growth of seagrasses in response to burial by migration of bedforms is combined with dating techniques to provide precise and rapid estimates of the migration speed of subaqueous dunes over seagrass patches. Two methods to estimate the time interval between the passage of successive dunes and the motion of single dunes through seagrass patches are described. The second method is more precise. The application of these methods to vegetated (*Cymodocea nodosa*) subaqueous dunes in the Alfacs Bay (NW Mediterranean) showed that the dunes traveled at an average speed of 13.0 ± 0.6 m yr⁻¹ and demonstrated that the methods can resolve migration speeds from 0.15 to 980 m yr⁻¹ with this particular seagrass species. In areas vegetated with different seagrass species, bedform migration can be estimated over different time scales. The strong coupling between seagrass and sediment dynamics resembles the coupling of vegetation and land dunes.

Large subaqueous bedforms are often present in shallow sandy marine environments (Amos and King 1984). These bedforms are often flow-transverse, repetitive structures that are referred to as subaqueous dunes (Ashley 1990). The terminology of large bedforms, which present a broad diversity of sizes and shapes, is confused (Amos and King 1984; Ashley 1990; Carter 1991), and the conditions that lead to the initial formation of these structures is uncertain (Carter 1991). There is broad consensus that the migration of these structures is an important component of coastal sediment dynamics (e.g. Carter 1991).

Empirical observations of the migration rates of subaqueous dunes are rare, probably be-

cause of the difficulties in measuring this process (e.g. Davidson-Arnott and McDonald 1989). Present techniques have improved the traditional method of comparing sequential bathymetric profiles (e.g. Langeraar 1966) with the use of electronic acoustic and positioning methods to increase their precision (Twichell 1983). Despite these improvements, the data obtained are still flawed by small (~1 m) positioning errors that may be of the same magnitude as the expected migration of the dunes. We describe a method, based on observations of the vertical growth of seagrasses in response to burial, to measure the migration of subaqueous dunes over time scales of months to years and demonstrate its power by describing the migration of subaqueous dunes in a deltaic bay.

Seagrasses are the dominant vegetation of shallow sandy bottoms in coastal areas around the world, particularly in tropical and subtropical areas where most of the species originated (den Hartog 1970). Seagrasses are clonal plants with a simple architecture (Fig. 1) based on a horizontal rhizome (equivalent to the shoots of trees or shrubs) buried (<0.01 to >0.6 m) in the sediment and vertical rhizomes (also referred to as short shoots) bearing the leaves and flowers positioned at regular intervals along the horizontal rhizome, as if they were trees laid on their sides (Duarte 1991). In addition to supporting the leaves and flowers, short shoots are responsible for the vertical growth of the plants (Patriquin 1973; Gallegos et al. 1993). Growth proceeds by adding internodes—the rhizome pieces separating the insertion points of successive leaves in the short shoot (Fig. 1).

By growing vertically, seagrasses react to sediment accretion and ensure that their active leaf-producing meristems, located at the tip of the short shoots, are maintained as close to the sediment surface as possible. The vertical

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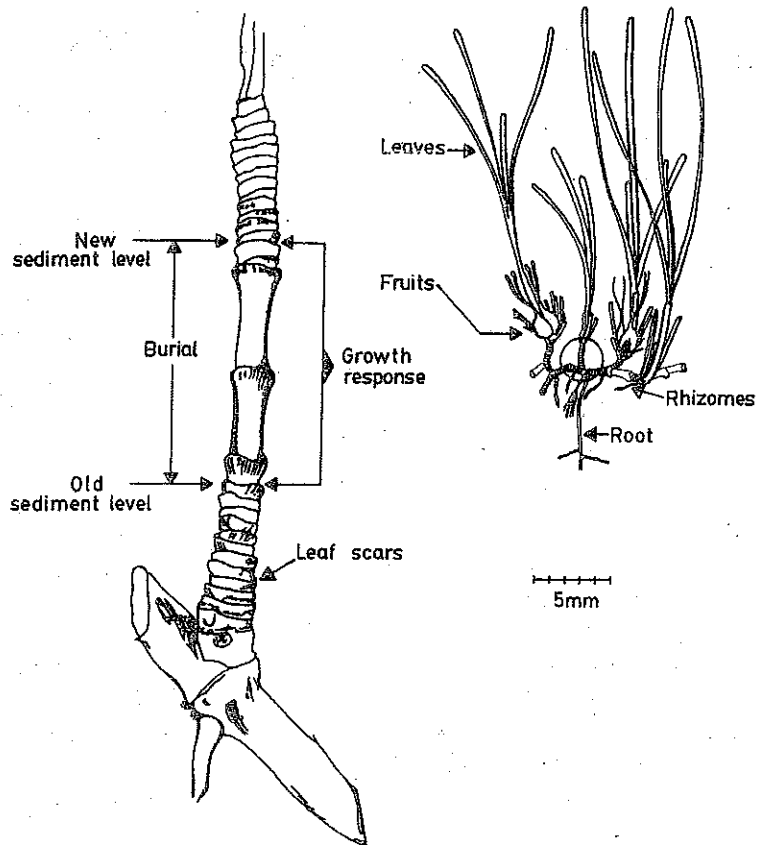


Fig. 1. Illustration of *Cymodocea nodosa* showing its different components and the details of the short shoots needed to estimate plant age and vertical growth.

growth rate responds to sediment accretion by relocating the leaf-producing meristems at the sediment surface (Fig. 1) and thereby closely matches changes in sediment accretion rates (e.g. Patriquin 1973), which suggests that seagrasses may be sensitive sensors of changes in the sediment level.

The suggested coupling between subaqueous dune motion and seagrass vertical growth would, if confirmed, parallel the demonstrated coupling between sediment accretion and plant growth on land dune vegetation (García-Novo 1979; Disraeli 1984). Pioneer land dune plants are rhizomatous monocotyledons, similar to seagrasses (e.g. Carter 1991), and they also react to burial by increasing vertical growth (e.g. Disraeli 1984). Coupling between land dune migration and vegetation dynamics is so strong that plant development has been used to infer dune migration rates. In particular, the age dis-

tribution of *Pinus pinea* along the sequence of tree burial and emersion associated with the migration of coastal dunes in the Doñana National Park (SW Spain) allowed the migration velocity of dunes to be estimated (García-Novo 1979).

The age of most seagrasses can be determined by counting the number of leaf scars and leaves on their shoots (Fig. 1) and multiplying these by the average time interval between the appearance of individual leaves (Patriquin 1973; Duarte and Sand-Jensen 1990a,b; Gallegos et al. 1992, 1993). The time intervals are referred to as plastochrone intervals (Erickson and Michelini 1957). The use of dating techniques to resolve time scales less than annual involves greater error because the plastochrone interval often varies seasonally (e.g. Sand-Jensen 1975). Yet, dating techniques have been used successfully to examine differ-

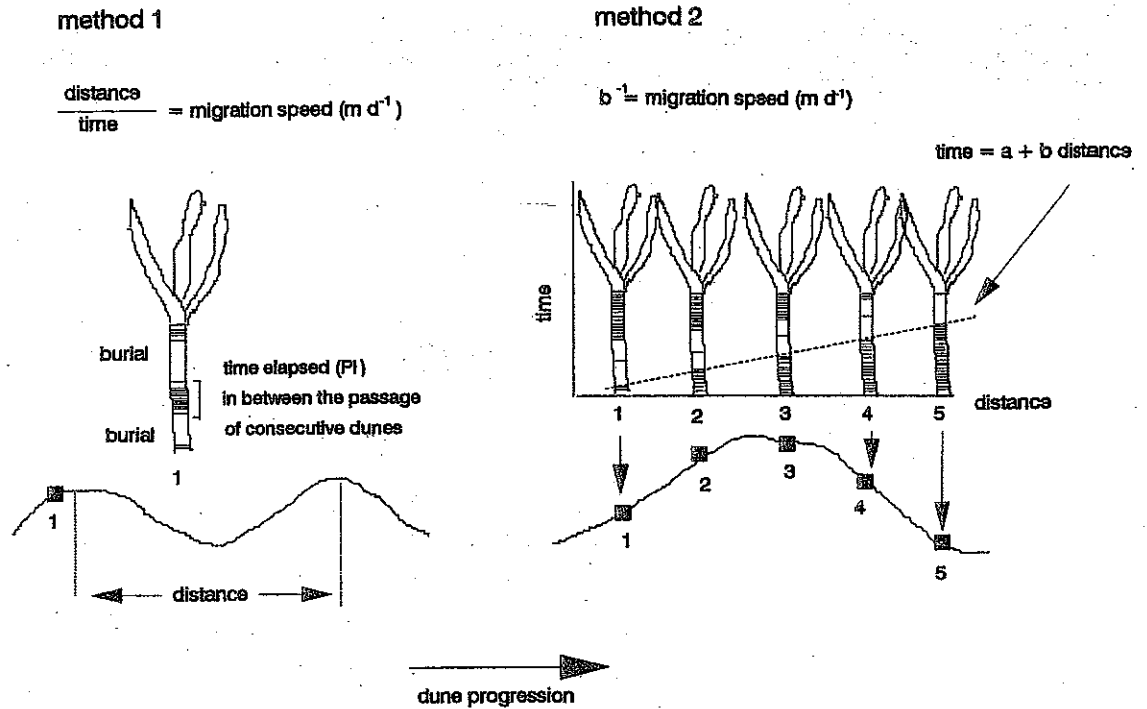


Fig. 2. Description of the bases and procedures used to measure subaqueous bedform migration over seagrass patches by the methods described here.

ent aspects of seagrass ecology such as leaf and flower production (Gallegos et al. 1992, 1993), colonization rates (Duarte and Sand-Jensen 1990a), and population dynamics (Duarte and Sand-Jensen 1990b). The potential of dating seagrass shoots to study sediment dynamics has already been demonstrated to elucidate the migration rate of "blowouts" or erosional scarps in meadows of the seagrass *Thalassia testudinum* Banks ex König (Patriquin 1975).

The history of the migration of subaqueous dunes over seagrass stands can be reconstructed from the marks left on the shoots as they are buried during passage of dune crests (i.e. elongated vertical internodes; Fig. 1) and using dating techniques to estimate the time elapsed since these marks appeared. The method can be applied in two different ways (Fig. 2). First, the time interval between the passage of successive dunes can be estimated by calculating the time elapsed between two consecutive periods of rapid vertical growth. Combined with the measured distance between successive dunes, these estimates allow the migration speed of the dune to be calculated. Second, the

time-course of transit of individual subaqueous dunes over seagrass patches (Fig. 2) can be followed by measuring the time lag between periods of rapid vertical growth in shoots sampled along the migration path of the subaqueous dune. The regression of the cumulative distance separating the shoots on the time difference between the growth periods is then calculated. The slope of the regression line gives an estimate of the average migration rate of the subaqueous dune.

The estimates of migration speed obtained applying these methods are apparent values, unless there is information about the direction in which the dune migrates. The deviation between true and apparent migration rate is a function of the cosine of the angle between the transect used to measure distance (i.e. the expected migration direction) and the true migration direction. The estimates obtained by the first method are less certain than those obtained with the second. The reasons are that the first method is based on a single determination of elapsed time since burial and assumes that the distance separating consecutive

subaqueous dunes remains constant, whereas the second method is based on multiple estimates of elapsed time since burial and is independent of the distance between adjacent dunes. The first method provides estimates of migration speed with fewer samples and allows more replicate estimates to be obtained per unit effort, yet is suitable for preliminary surveys before application of the more precise second method. The precision of either method can be improved by increased replication.

We use the seagrass *Cymodocea nodosa* Ucria Aschers., a common seagrass species on the Mediterranean and NW African coasts (den Hartog 1970), to estimate the migration rate of subaqueous dunes in Alfacs Bay by our two methods. Alfacs Bay is a shallow, sandy (medium grain size, $\sim 265 \mu$ or 2.2 ϕ , Capaccioni 1988) embayment in the Ebro delta ($40^{\circ}40'N$, $0^{\circ}40'E$; Fig. 3) formed ~ 400 yr ago by the erosion of the southern lobe of the ancient delta (Maldonado 1972). The bay has an area of 56 km^2 and is separated from the Mediterranean Sea by a 5 km long, 300 m wide sand barrier (Fig. 3). The sand barrier slopes gently into the bay where large-scale bedforms of different wavelengths develop (Fig. 3). These bedforms correspond, because of their shape, height, and spacing, to 2-D megaripples according to the classification of Amos and King (1984) or medium-size subaqueous dunes according to that of Ashley (1990). We refer to them as bedforms or subaqueous dunes hereafter.

The bedforms are covered by scattered patches of *C. nodosa*. Previous research (Duarte and Sand-Jensen 1990a) focused on plant patch dynamics has provided evidence that subaqueous dunes are highly mobile and that the dynamics of the *C. nodosa* patches are closely linked to their migration. The migration of subaqueous dunes should lead to increased vertical growth at the progradational lee face where plants are being buried, to a reduction in vertical growth as the dune crests move over the plants, and to plant mortality at the regressing slope of the dunes where erosion exposes plant rhizomes which subsequently die (Duarte and Sand-Jensen 1990a).

Between May and July 1991, we established three 100-m transects perpendicular to the axes of the subaqueous dunes (i.e. parallel to the anticipated direction of migration, Fig. 3). We

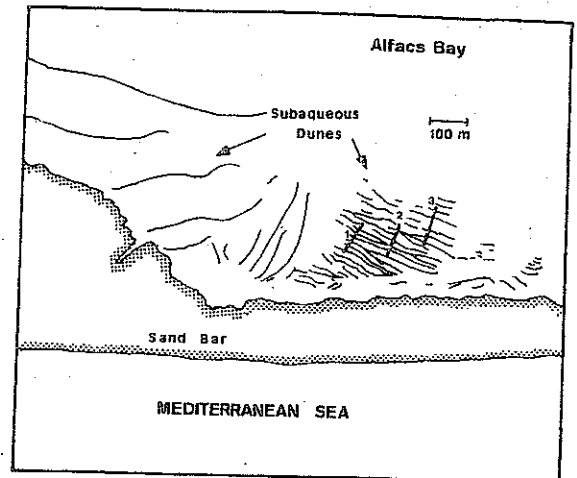


Fig. 3. Outline of the study area of the subaqueous dunes studied and the position of the transects (transcribed from an areal photograph).

then measured depth at 1 ± 0.01 -m intervals along the transects and carefully collected all *C. nodosa* short shoots within a 0.01-m^2 quadrat or 0.25 m^2 , if the shoot density was $< 2,000$ shoots m^{-2} at 1-m (one transect) or 2-m (2 transects) intervals. We then selected the five oldest short shoots in each sample and measured the sequence of their internodal lengths (to the nearest 0.1 mm) under a dissecting scope at 60 magnifications. We averaged the internodal lengths of similar age of the shoots measured to obtain a time series of average internodal lengths (i.e. average vertical growth rate at each position sampled). Time units are reported as leaf plastochrone intervals (PI, the time interval between the appearance of consecutive leaves) and as chronological time, calculated by multiplying time in PIs by 26 d, the average time interval ($SE \pm 1$ d) between the appearance of successive leaves in *C. nodosa* short shoots (Duarte and Sand-Jensen 1990b).

The subaqueous dunes were ~ 0.22 m high (range 0.07–0.65 m) and the distance between them was, on average, 21 m (range 7–29 m) (Fig. 4). The asymmetry of the bedform suggested that the dunes migrated from the open bay toward the sand barrier, because the slopes facing the sand barrier tended to be steeper than those facing the open bay which is characteristic of the depositional slip face of the dunes (Fig. 4). Plant cover consisted of patches 18 m long (range 2–70 m) initiated over the

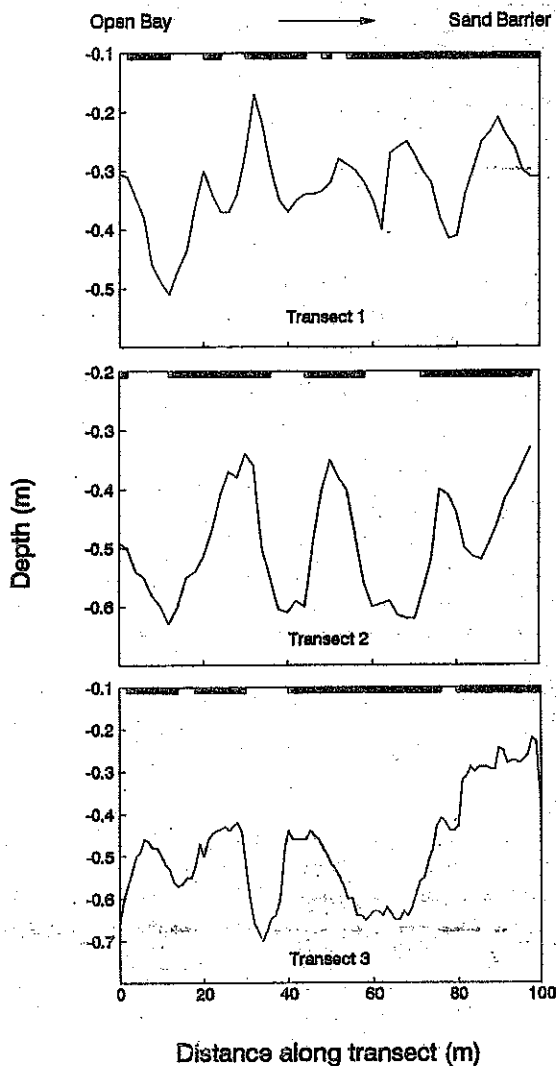


Fig. 4. Sediment profile along the transects. Solid bars show the areas covered by *Cymodocea nodosa* patches.

lee slope of the subaqueous dunes (i.e. that facing the sand barrier) and ending in exposed, dead rhizomes at the opposite slope facing the open bay, confirming that the bedforms migrate from the open bay toward the sand barrier (Fig. 4).

Many of the shoots collected showed two periods of high rates of vertical growth (Fig. 5), resulting in internodes several-fold greater than those of shoots in stable areas. The presence of successive periods of high vertical growth revealed the passage of several dunes

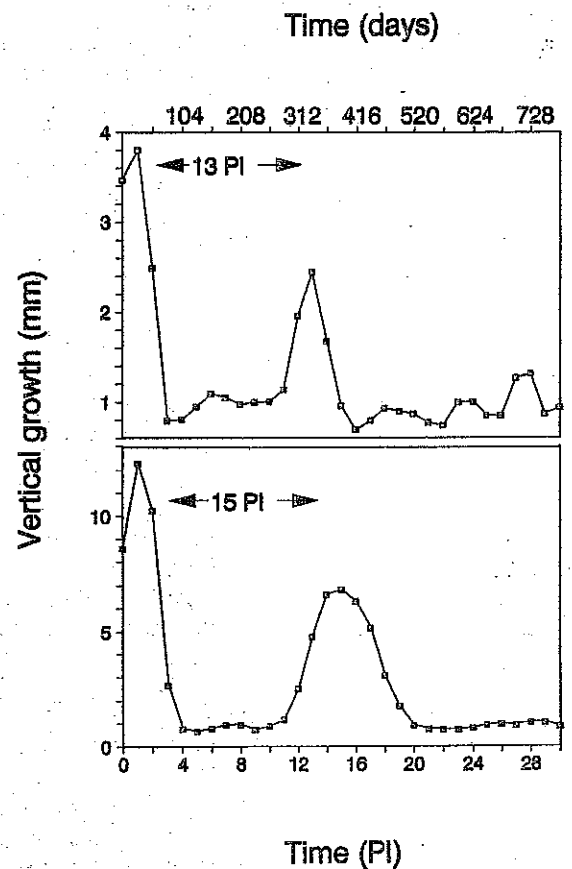


Fig. 5. The sequence of average vertical growth along two average *Cymodocea nodosa* short shoots, showing two periods that correspond to the passage of consecutive subaqueous dunes.

over the shoots, which allowed us to apply our first method. The results indicate that subaqueous dunes move at an average (\pm SE) speed of 1.82 ± 0.11 m (PI) $^{-1}$ or 25.6 ± 1.5 m yr $^{-1}$ (No. of observations, 75). Individual estimates ranged between 0.53 and 4.25 m (PI) $^{-1}$, i.e. 7.5 and 59.6 m yr $^{-1}$. Each of these velocity estimates is based on a single estimate of transit time and often encompasses time periods < 1 yr (mean, 10.7 PI; range, 4–17 PI, compared to 14 PI in a year). The variability of these individual estimates of migration speed can be partially attributed to seasonal changes in the duration of the plastochrone interval.

The second method produced estimates of the migration speed over observational time scales of up to 3 yr (Fig. 6). The estimates

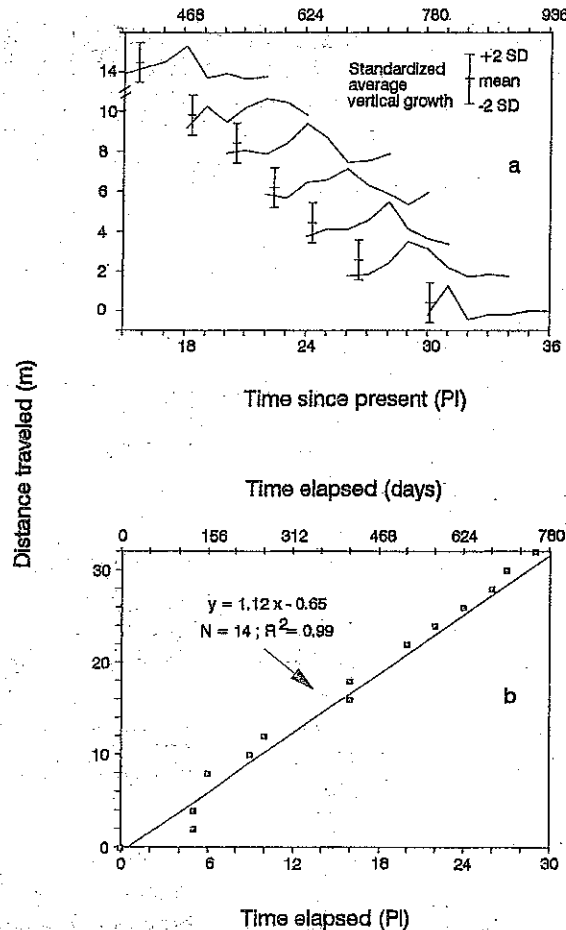


Fig. 6. [a.] Three-dimensional representation of the records of subaqueous dune passage over individual locations. The y -axis shows the position of the plants sampled at successive sampling stations along the transect; the x -axis represents the time sequence of average vertical growth [represented on an independent axis as standardized values, 0 ± 1 (mean \pm SD), to avoid differences in scale] of the *Cymodocea nodosa* short shoots. The time lag in the appearance of the vertical growth maxima gives the time sequence of the passage of the subaqueous dune across the transect. [b.] Regression analysis of the time elapsed for the subaqueous dune to travel from one station to the next against the distance between the stations gives the migration speed of the subaqueous dune.

obtained were much more precise with a C.V. of individual estimates = 30% (Fig. 6). We were able to follow the passage of 37 dunes over plant patches, resulting in 336 individual estimates of distance traveled per unit time. The averaged estimates allowed a close relationship to be constructed between the average dis-

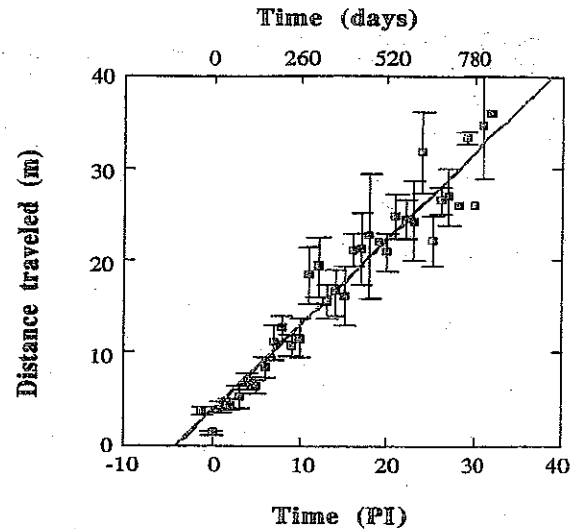


Fig. 7. The relationship between the average distance traveled by subaqueous dunes and the time elapsed, as inferred by averaging all individual estimates as shown in Fig. 6. Symbols represent the distance traveled by subaqueous dunes, averaged per plastochrone interval; bars extend ± 1 SE of this average value.

tance traveled by the dunes and the time elapsed (Fig. 7), as described by the regression equation.

$$\text{Distance traveled (m)} = 3.74 + 0.93 (\pm 0.044) \text{ time (PI)}$$

($R^2 = 0.93$; $N = 34$; $P < 0.0001$). The slope of the regression line indicates that average dune migration speed is $13.0 \pm 0.6 \text{ m yr}^{-1}$ [i.e. $0.93 \text{ m (PI)}^{-1} \times 14 \text{ PI yr}^{-1}$]. This estimate is significantly slower than that obtained with the first method ($25.6 \pm 1.5 \text{ m yr}^{-1}$). The disagreement between the two methods is attributed to the greater accuracy of the second, which is also very precise (SE of the mean migration velocity $\pm 0.6 \text{ m yr}^{-1}$).

The second method is simple and produces reliable estimates of migration speed compared to the first, which is much less accurate and precise, but is even less expensive. Standard sampling theory (Am. Public Health Assoc. 1985), assuming normally distributed values, indicates that triplicate estimates of dune migration speed based on the first method would have yielded velocity estimates within 50% of the mean migration velocity. This low resolution may be acceptable in preliminary

large-scale surveys. Both methods are subject to error derived from error in dating the plant material, which is ~5% of the mean for this species and location when growth is examined at annual scales (Duarte and Sand-Jensen 1990b). This small error allows the precision in estimating the migration of vegetated subaqueous dunes obtained with the second method.

The two methods proposed here should be applicable to bedforms vegetated by most other seagrass species, except for the genera *Zostera* sp. L., *Heterozostera* sp. (Setchell) den Hartog, and *Halophila* sp. Du Petit Thouars (which cannot be dated because they lack vertical rhizomes). These plants cannot grow vertically and are unlikely to thrive in areas with substantial sediment motion. The species that are suitable for these methods encompass 8 of the 12 seagrass genera that are ubiquitous in the Mediterranean and Caribbean Seas and in the Indian and West Pacific Oceans (den Hartog 1970). Moreover, different species can be used to examine sediment dynamics at different time scales. The time scales are set by the duration of the plastochrone interval and the lifespan of the shoots. For instance, the use of *C. nodosa* should, in principle, allow measurements of bedforms traveling at minimum rates of 1 m in 7 yr (the lifespan of the shoots, Duarte and Sand-Jensen 1990a) and at maximum rates of 70 m (i.e. maximum patch length) during a plastochrone interval, corresponding to migration speeds of 0.15 and 980 m yr⁻¹, respectively. Shoots of small seagrasses have shorter plastochrone intervals and lifespans than shoots of large seagrasses (Duarte 1991) and should therefore be appropriate to measure bedforms with fast migration rates. Because some areas, notably Indo-Pacific tropical and subtropical coastal zones, have diverse seagrass floras, different species (small and large) can be used to examine bedform migration at different time scales simultaneously.

In summary, dating techniques and measurements of the vertical growth rate of seagrass short shoots can be used to estimate the migration speeds of large-scale bedforms over vegetated, shallow coastal areas. The use of these techniques should increase the existing empirical database to testing models of sediment transport in the coastal zone. Application

of these simple methods demonstrates the strong coupling that exists between seagrass growth and sediment transport and extends the observation of close coupling between transport rates and vegetation growth of coastal dunes to the adjacent subaqueous environment.

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