CHAPTER 7.
HERDING

7.1. Introduction

Our understanding of the social behaviour of dugongs is conspicuously deficient (Anderson, 1981a; Marsh, 1989a; Nishiwaki and Marsh, 1985). The habits and habitats of dugongs usually make them difficult to observe (Bertram and Bertram, 1973), and even when they can be watched, the lack of distinct size classes (Marsh, 1980) or obvious sexual dimorphism limits the data obtained.

Information on herding in dugongs has come from aerial survey and incidental sightings or ethno-biological sources. Dugongs are most frequently seen in groups of one or two, but large groups of up to several hundred animals have been reported (see below). The demographic structure of dugong herds is unknown, although there is some evidence that large herds may contain a high proportion of females, calves and young males (Anderson, manuscript; Marsh, 1989c; Smith, 1987). Aboriginal and Islander hunters in Australia believe that dugong herds are controlled by leaders (Johannes and MacFarlane, 1991; Roughsey, 1971; Smith, 1987) and Anderson and Birtles' (1978) and Anderson's (1982b) interpretation of some observations support this belief. Indigenous hunters disagree about the sex of presumed leaders (see Johannes and MacFarlane, 1991), and there is no information on the sex or age structure of dugong herds. (The large collection of salvaged dugongs maintained at James Cook University [Heinsohn, 1972; Marsh 1980; Marsh et al., 1984a, b and c] provides data on the demographic structure of dugong populations, but not herds). The functions of herding in dugongs have not been investigated and nothing is known of the seasonality of dugong aggregations.

The aims of this section were to document the gregariousness of dugongs in Moreton Bay, and secondarily, to document the distribution of calves in the population.

7.2. Methods

Data on the size of dugong herds in Moreton Bay were collected during 28 aerial surveys of the East and West study areas. The details of these surveys are described in section 5.2.1 and the specifications of each survey are presented in Table 5.1.

The principal aims of those surveys were to obtain accurate counts of the dugongs visible in the study areas, and to translate the spatial distribution of sightings accurately onto a habitat map. The dugongs frequently formed large, obvious herds, composed of one to several groups, which often spread over areas of 0.5 km^2 or more. The aims of the aerial surveys dictated that the dugongs in large herds be recorded in the smallest groups that could be counted within the time constraints imposed by the aerial surveys. Hence, large herds were usually counted (and/or photographed) and plotted as a series of more-or-less discrete groups. The distribution of each recorded group of dugongs is plotted for each survey in Figure 5.1b. To measure herd size, those groups that were part of a larger herd had to be re-assembled. In fusing groups back into herds, I was guided by the original field maps, which usually indicated which groups appeared to be part of a herd. A total of 1,197 recorded groups were fused into 1,069 herds.

If dugong herds are more than coincidental assemblages (see below), then it may be more relevant to consider the size of the herd in which the average dugong occurs ('typical' herd size) than the mean herd size. As demonstrated by Jarman (1974), the 'typical' herd size may differ substantially to the mean herd size. Following Jarman (1974), 'typical' herd size is derived by adding up the size of the herd in which each individual occurred, and dividing by the total population:

$$\frac{n_1^2+n_2^2+n_3^2+....n_i^2}{N}$$

where n_1 , n_2 ... n_i are the number of dugongs in each group and N is the total count of dugongs. This index gives relatively more weight to large than small herds.

As described in section 5.2.1.3, calves were defined as individuals that were distinctly smaller than the dugong with which they were closely associated.

7.3. Results

7.3.1. Herd size

Figure 7.1 shows the frequency distribution of herd size-classes during each survey period. Most herds were very small, but most dugongs occurred in very large herds. Nearly 53% of all herds contained one dugong (Figures 7.1 and 7.2), but herds of one dugong accounted for just 5.5% of all dugongs sighted (Figure 7.2). While 88% of herds contained five or fewer dugongs, 85% of dugongs occurred in herds of more than five animals (Figure 7.2).

Mean herd size was highly correlated with 'typical' herd size ($n = 28$, $r = 0.8236$, $p = 0.0000$; Figures 7.3b and c). However, due to the highly skewed nature of the distribution of herd sizes (Figure 7.1), the mean herd size (9.7 dugongs; Figure 7.3c) differed substantially from the 'typical' herd size (146.9 dugongs) and the median herd size (140 dugongs; Figure 7.2). A herd of at least 100 dugongs was sighted on 27 of the 28 surveys, and a herd of over 200 was seen on 11 of the 28 surveys (Figure 7.3a). The largest herd contained 459 dugongs.

The largest herds were observed during spring and summer (Figure 7.3), however, neither the 'typical' nor mean size of herds in each survey varied significantly between seasons or between years, and there were no year by season interactions (Table 7.1).

Both 'typical' and mean herd size were correlated with the total number of dugongs seen on each survey (respectively, $n = 28$, $r = 0.7659$, $p = 0.0000$ and $n = 28$, $r = 0.5731$, $p = 0.0014$; Figure 7.3). However, neither was correlated with survey conditions (described in section 5.2.2.1; Spearman Rank correlations, respectively, $n = 28$, $r = 0.2470$, $p = 0.2051$ and $n = 28$, $r = -0.0025$, $p = 0.9899$).

7.3.2. Proportion of calves

Averaged across all surveys, calves represented 10.1% of the dugong population in the study areas. Although the overall proportion of calves seen on each survey did not vary significantly between seasons or years (and there was no year by season interaction; Table 7.2; Figure 7.3d), my boat-based observations showed that there was a distinct calving season in Moreton Bay. New-born calves were seen from September through January, but mostly between October and December.

Even when surveys were grouped into a post-calving period (December - March) and another period (April - November), no significant difference in the proportion of calves seen on each survey was detected (Table 7.3). However, the slope of the regression of the number of calves (dependent variable) against herd size (for herds > 1) was significantly steeper during the post-calving period than during the rest of the year (t-Test: $t = 3.3103$, $df = 497$, $p = 0.0005$). This result indicates a higher proportion of calves in herds during the post-calving period than during the rest of the year (regressions:

[1] number of calves = 0.3471 + 0.0977 * herd size

$df = 130$, $F = 1577$, $p = 0.0000$, $r^2 = 0.9233$

[2] number of calves = 0.3993 + 0.0878 * herd size

$df = 367$, $F = 2722$, $p = 0.0000$, $r^2 = 0.8808$).

The tight, linear relationships between the number of calves in herds and herd size (for herds of more than 1) indicates that the proportion of calves did not vary with herd size. Furthermore, herd size was not significantly larger during the post-calving period than during the rest of the year (Table 7.3).

There was no correlation between the proportion of calves seen on each survey and the survey conditions (Spearman Rank correlation: $n = 28$, $r = -0.1660$, $p = 0.3985$)

7.4. Discussion

7.4.1. Herds: feeding assemblages or social groups?

In Moreton Bay, feeding dugongs can be highly gregarious. During aerial surveys, 80% of dugongs were sighted in herds of more than 20, and 31% occurred in herds of over 200 dugongs (Figure 7.2). Calculated across all surveys, the 'typical' herd size, the size of herd in which most dugongs occurred, was 147 dugongs.

Despite this gregariousness, little is known of the structure or function of the herds. The aerial surveys were all flown around high tide, when the dugongs were most likely to be on the banks and feeding. Because of this bias, it is difficult to eliminate the possibility that the observed herds were simply feeding aggregations. Substantial benefits could accrue to individual dugongs by feeding in a large herds (section 6.6.3).

If the observed herds were solely feeding assemblages, then they should disperse during low tide, when the dugongs had less access to their seagrass feeding areas. Some herds that I observed (from a boat), however, persisted through the low tide periods, and dugongs travel to and from feeding areas in groups (Anderson and Birtles, 1978; pers. obs.). These observations suggest that dugong herds may be more than just feeding assemblages. My observations of the interaction and coordination of dugongs within herds suggest that the herds may also have a social function. In response to within-herd stimuli (eg. a behaviour I have interpreted as an alarm signal), dugongs within a distance of 150 m can respond in a cohesive and coordinated manner (see Preen, 1989b). In response to 'external' stimuli (eg. a passing speed boat) originating as far as 1 km away, the herds can respond in a coordinated manner, displaying directional sensitivity to underwater sounds. Dugongs produce a diverse suite of under-water sounds (Preen, unpublished data), as well as some distinctive behaviours by which they appear to communicate (pers. obs.).

Some Australian Aborigines and Islanders believe that dominant dugongs, known as 'whistlers' (because of the sound they make), control herds (Bradley, 1991; Johannes and MacFarlane, 1991; Roughsey, 1971; Smith, 1987). However, the 'whistlers' that I have observed appeared simply to have a respiratory impediment that caused them to produce a hollow whistle during inhalation, and never effected an observable response from nearby dugongs.

Other evidence that herds are more than feeding assemblages includes echelon-formation swimming (Nishiwaki and Marsh, 1985; pers. obs.) and possible defensive behaviour by large individuals in a herd following disturbance by a boat (Anderson, 1981a, 1982b).

7.4.2. Stability of herds

The herds of dugongs were often composed of smaller groups, a pattern of association that has been reported for pelagic dolphins (Scott and Chivers, 1990) and many large African grazing mammals (Leuthold, 1977; Murray, 1981; Mloszewski, 1983; Sinclair, 1977). The membership of these groups, and indeed the herds, of dugongs appears to be quite open. Relatively brief observations of herds during aerial surveys suggest plasticity of herd composition: individuals and cow-calf pairs were often seen to split from a group within a herd, or to come from some distance to join a herd. Anderson and Birtles (1978) comment that (small) dugong groups may break up and reform during a day. The large herds formed by ungulates are also typically open (Murray, 1981).

Unlike the Moreton Bay dugongs, Florida manatees only form large aggregations at warm water refuges (see below). During other times of the year they form loose transient associations (Rathbun and O'Shea, 1984). Hartman (1979) considered the social bond of manatees to be highly unstable, and that all associations (except the cow-calf and the mating or oestrous herd) to be temporary groupings. He observed few animals that stayed together for as long as a day. Tiedemann (1979) found that manatee groups were more likely to remain together for less that 15 minutes than for longer than 15 minutes.

7.4.3. Calves and herds

As for most group-living species (Myers, 1983; Murray, 1981), nothing is known of the social relationships between individual dugongs within herds, apart from the cow-calf relationship. Similarly, the number of calves in dugong herds is the only information available on the age structure of herds. Yet calf counts can be an imprecise measure of the number of calves in a herd or population. In Moreton Bay, just over 10% of the dugongs sighted were categorised as calves, but the proportion varied from 7.1-15.9% on different surveys (Figure 7.3d). This variation was not due to the recruitment of calves (Table 7.3), and it was not due to differences in survey conditions (section 7.3.2). In one instance, the estimated percentage of calves changed significantly, from 7.1% to 13.9%, between sequential surveys separated by 13 days and conducted under good to excellent conditions (Figure 7.3d; $X^2 = 7.191$, df = 1, p = 0.0073).

The proportion of calves recorded by other surveys from throughout the dugong's range varied from 1 to 24% of the observed population (Table 7.4). From these data, it is apparent that the percentage of observed calves tends to decrease with increasing survey altitude (Table 7.4), although due to the small number of altitudes (4), the strong correlation was not significant ($r = -0.9358$, $n = 4$, $p = 0.0642$). Small calves are more difficult to see from higher altitudes. In Moreton Bay, most dugongs occur in herds, and most large herds were photographed, so the calf counts are likely to be more accurate than most other surveys flown at 275 m. This conclusion is supported by Table 7.4.

Within the limits of their accuracy, calf counts provide an integrated measure of recruitment over several years. Following standard practice, calves are defined as individuals distinctly smaller than the dugong with which they were closely associated. Dugongs have a calving interval of 3-7 years and calves may suckle for at least 1.5 years (Marsh et al., 1984a). On several occasions I have seen a new calf with its mother and a (presumed) penultimate calf.

Assuming that the chance of sighting a calf is independent of herd size, the tight, linear relationship between the number of calves and herd size suggests that large herds do not attract cows with calves. This is despite the fact that the risk of predation is greatest during the post-calving period. Of the 33 large sharks (2-4 m) sighted during surveys, 91% were seen on the eastern banks during the post-calving period (December - March). The incidence of shark attacks on Bottlenose dolphins (Tursiops truncatus), especially females with very young calves, peaks in Moreton Bay during this period (Corkeron et al., 1987). This result suggests either that dugong herds do not function to reduce the risk of predation, or that the calf counts fail to resolve the relationship between herd size and the incidence of young calves due to the inclusion of calves from more than one seasons recruitment in the counts.

7.4.4. Herd size in dugongs

Jonklass (1961) believed dugongs to be solitary. Jarman (1966) reported that dugongs were generally seen in small parties of two or three and suggested that occasional herds resulted from the joining of family groups. No evidence has yet been collected to support pair bonding, and what is known of the mating behaviour of dugongs (Anderson, manuscript; Preen, 1989b) makes it unlikely. Large herds, however, do sometimes form. Annandale (1905), citing local fishermen from the Gulf of Manaar in India, stated that flocks of many hundreds formerly occurred in the area. Saville-Kent (1900) describes dugongs as essentially social, assembling in herds of six to 40 or more. Bertram and Bertram (1973) quote Travis' (1967) improbable account of droving large herds of dugongs along the Somali coast, as though they were domesticated cattle. Travis claims herds of up to 500. Welsby (1905, p. 100) describes a large herd he saw in Moreton Bay in 1893: "... a herd of these animals three miles in length ... at no time were there less than twenty or thirty spouting simultaneously ... and in width they extended about three hundred yards".

A more contemporary, and perhaps more accurate assessment of dugong herding patterns is provided by the results of aerial surveys from throughout the dugong's range (Table 7.5). Mean and maximum herd sizes have been presented, but it was not possible to extract the data necessary to calculate 'typical' herd size. The data have been arranged by survey type, as it is more likely that the full extent of dugong herds is not recognised during strip-transect surveys (due to the restricted transect width and lower flying height) than shoreline surveys.

It is apparent that the maximum herd size and the mean herd size recorded from most areas are much smaller than recorded from Moreton Bay. Although some of the listed surveys covered the world's best known dugong areas (eg. Cape Flattery-Princess Charlotte Bay (including the Starke River area), Torres Strait, Shark Bay, Northern Territory), distinct herds of 100 or more dugongs have been recorded from only four areas: Moreton Bay, Shark Bay, Arabian Gulf and Starke River area, Cape York. Despite several surveys in each area, discrete herds of 100 or more dugongs have been seen only once each in Shark Bay, the Arabian Gulf and the Starke area.

Spencer (1989) has compiled a list of incidental sightings of dugongs along the Queensland coast (1973-1988) including four years of reports from Coastal Surveillance (Coastwatch) flights along the eastern shoreline of Cape York, north of Cairns. Coastwatch aircraft survey the nearshore waters on a daily basis. Acknowledging the limitations of the coastwatch data (sightings, especially of small groups, were not always recorded; Spencer, 1989), it is significant that herds of 100 or more dugongs were reported on only seven occasions (Spencer, 1989). Given the frequency of the Coastwatch flights (approximately daily for four years), the favourable location of their flight path in relation to dugong habitat in the Cape Flattery-Princess Charlotte Bay region (including the Starke area), these data suggest that large herds of dugongs in tropical Queensland are comparatively rare. Although the formal dugong surveys in most areas have been seasonally restricted, it is clear from Table 7.5 that surveys have been conducted in different areas in almost all months. Furthermore, the Coastwatch surveys were conducted in every month. Hence, this timing bias may not be significant.

In Moreton Bay, herds of 100 or more dugongs were seen on 27 of 28 aerial surveys (on survey 10, 66% of the estimated population was missed, and the largest herd that was seen contained only 70 dugongs; Figure 7.3a). Herds of 200 or more dugongs were seen on 11 of the 28 surveys (Figure 7.3a). It is apparent that the herding behaviour of dugongs in Moreton Bay differs substantially from other areas that have been investigated.

Anderson's (1982a, p. 82) assessment that dugongs are "essentially gregarious, though frequently solitary" is supported by the now considerable body of aerial survey data. Although, with reported herd sizes ranging from 1 to 674 (Preen, 1989a), and mean herd sizes as small as 1 (Heinsohn and Marsh, 1979) and as large as 81 (Figure 7.3c), dugongs may best be considered as facultative herders.

Florida manatees also regularly form large aggregations, occasionally containing 200-300 individuals (Reynolds and Wilcox, 1986). Their herding behaviour contrasts with that of dugongs in that the large aggregations are always environmentally induced. Aggregations of manatees occur around warm water sources (natural springs and power station outfalls) during cold periods in winter (Packard et al., 1989; Reynolds and Wilcox, 1985, 1986). Away from the warm water refuges, manatees are described as "mildly social, essentially solitary" (Hartman, 1979, p. 95), although most manatees seen on aerial surveys were in groups of more than one (Irvine et al., 1981). Reynolds (1981) considered manatees to be moderately social. Reported mean group sizes range from 1.9 (Irvine et al., 1981) to 3.0 (Odell, 1980 cited in Reynolds, 1981). Hartman (1979) recorded a maximum group size of nine during non-winter aerial surveys. Lefebvre and Powell (1990) recorded a maximum group size of six, although 54% of the cumulative total of 215 manatees were solitary.

Generalising from surveys conducted throughout their range (east Africa, Arabia, Micronesia, Melanesia and Australia), dugongs typically occur in small herds (less than 10, often much smaller), although they occasionally aggregate into herds of up to 100 or more (references in Table 7.5 plus: Anderson and Birtles, 1978; Brownell et al., 1981; Heinsohn and Wake, 1976; Hughes and Oxley-Oxland, 1971; Ligon, 1976; Ligon and Hudson, 1977; Marsh et al., 1992; Prince, 1986; Robineau and Rose, 1982; Rathbun et al., 1988). Moreton Bay, where 60% of dugongs occurred in herds of more than 100, is the only known substantial exception to this generalisation.

7.4.5. Why does the herding behaviour of dugongs in Moreton Bay differ from other areas?

The alternate question 'why don't dugongs from other areas routinely form large herds?' may be more informative, as Moreton Bay is at the edge of the dugongs' range. Given the state of our knowledge of dugong ecology and social behaviour, this question requires some speculation, and definitive answers will not be possible.

Among the most important variables which determine the size of animal groups are (1) the openness of the terrain, (2) predation pressures and (3) the availability and distribution of resources (Alexander, 1974). Although the first factor is really a sub-set of the second, I will consider each of these variables as possible explanations of herding in dugongs. Because of the limited data on dugongs, I consider them in relation to the existing theoretical framework describing large grazing ungulates.

7.4.5.1. Cover

Predation can be a potent determinant of social behaviour (Alexander, 1974; Estes, 1974; Hamilton, 1971; Jarman, 1974; Norris and Schilt, 1988; Parrish, 1989; Pulliam and Caraco, 1984), and Geist (1974) hypothesised that the anti-predator behaviour of ungulates is, in part, a function of the cover provided by their habitat. Drawing on the observation that virtually all bovids which live away from thick vegetation cover are social, while virtually all solitary species depend on concealment, Estes (1974) suggested that gregariousness is an essential adaptation for life in the open. Hence, in habitats with little or no cover, ungulates use each other as orientation points and as cover (Geist, 1974). This response, according to Geist (1974) explains why species usually considered to be solitary congregate in large herds when, on rare occasions, they feed in open areas.

Dugongs most commonly occur in tropical inshore habitats (Heinsohn et al., 1977), which are often characterised by terrigenous sediments and relatively turbid waters (Bayliss, 1986). The turbidity of the water can be substantially increased by the plumes of sediment (Anderson and Birtles, 1978) that result from the furrowing method of feeding typically adopted by dugongs (Heinsohn et al., 1977). Consequently, visibility within these habitats is often very poor. The re-suspension of sediments may also liberate many scents. Turbid water may, therefore, provide a type of visual and olfactory cover for dugongs, offering them some protection from predators, as it can for fish (Hanekom and Baird, 1984 cited in Bell and Pollard, 1989). Under such circumstances dugongs may be under little selection pressure to associate in large herds to reduce the risk of predation.

In contrast to most dugong habitats, the eastern banks in Moreton Bay are usually characterised by clear water and the seagrass grows on virtually pure sand . Hence, the opportunity for protection by visual obscurity and olfactory 'noise' is reduced, and the formation of large herds may be advantageous. This explanation of the gregariousness in dugongs, however, does not explain all situations. For example, parts of Shark Bay, which supports a population of over 10,000 dugongs (Marsh et al., 1991) has clear water (pers. obs.), as do some reef habitats inhabited by dugongs, but large herds are not characteristic of these populations.

7.4.5.2. Predation

The above argument assumes that predation pressure has an important influence on the survival and reproduction of dugongs. But risk of predation is related to body size, and it seems that dugongs outgrow most predators. In this regard, adult dugongs may be like elephants, rhinoceroses and hippopotami (Owen-Smith, 1988). The dugongs' large mass, fusiform shape, bottom living habits and thick hide (Nishiwaki and Marsh, 1985), which becomes very tight and tough under stress (Johannes and MacFarlane, 1991), make adult dugongs unassailable to all but the largest predators. Anderson (1981b) shows a photo of a dugong with a healed scar from the bite of a large shark. Very large sharks are rare, and because of differences in preferred habitats dugongs would rarely encounter killer whales (<u>Orcinus orca</u>) and crocodiles (<u>Crocodilus porosus</u>), known predators of dugongs (Anderson and Heinsohn, 1978; Anderson and Prince, 1985; H. Marsh; pers. comm.). Observations of attacks by sharks under natural conditions in Torres Strait, where dugong hunters have a keen understanding of dugong behaviour, are very rare (Johannes and MacFarlane, 1991). Nietschmann and Nietschmann (1977), however, report that Islanders have seen sharks attack young dugongs. Similarly, Aborigines from eastern Cape York state that adult dugongs die only from disease and old age, but young dugongs are killed by sharks and crocodiles (Smith, 1987).

The fact that predation of adult dugongs is probably not a common threat is supported by the abundance of solitary dugongs seen in Moreton Bay (Figure 7.1), even though close encounters with sharks are common. During the aerial surveys, large sharks (2-4 m) were seen within 200 m of dugongs (and as close as 100 m) on 12 occasions. Six of the 13 satellite transmitters, which were attached by a 3 m tether to dugongs, were attacked by sharks.

Marsh et al. (1984a) have demonstrated that the survival of adult dugongs must be very high (at least 90% of females over 4 years old need to survive each year) and that the survival of calves is a critical factor determining the stability of a dugong population. These findings imply that while predation of adults is uncommon, it may be common in juveniles. I was unable, however, to detect evidence of predator avoidance behaviours by cow-calf pairs in Moreton Bay. Although the risk of predation was apparently greatest during the summer season, when calves are small and sharks are most abundant (section 7.4.3), dugong cows with young calves did not seek larger herds for protection, as the relationship between herd size and the number of calves remained linear. This result, however, may reflect a lack of resolution in the calf counts during the aerial surveys.

Jarman (1974) predicts a seasonal increase in herd size in some antelope as a result of the increased risk of predation during the calving season. However, the size of dugong herds did not significantly change between climatic seasons (Table 7.2) or between post-calving and other periods (Table 7.3).

These data suggest that predation is unlikely to be a significant reason for the observed herding of Moreton Bay dugongs, and in the absence of comparative data on predator abundance, risk of predation cannot explain the difference in herding behaviour between regions.

7.4.5.3. Resources

Resource quality, predicability and spatial variance interact to influence group size in many species (Pulliam and Caraco, 1984). For example, in grazing ungulates, herd size can vary greatly, depending on the availability (Geist, 1974; McNaughton, 1984) and dispersion of food (Jarman, 1974; Sinclair, 1977; Taylor, 1989).

Seagrasses in a sub-tropical area (like Moreton Bay) have predictable seasonal changes in abundance and productivity (section 4.4), while the availability of tropical seagrasses can be unpredictable, due to significant inter-year variation (Lanyon, 1991). Geist (1974) predicts that herding behaviour in ungulates would develop where the exploited plant communities were stable, self-regenerating and predictable, as these conditions would select for the retention of juveniles within the social unit. Geist (1974) also suggests that predictable periods of vegetative productivity would shorten birth and rutting seasons, and lead to the intensification of rutting activities. These predictions are supported by the limited comparative data on dugongs from tropical and sub-tropical areas. In Moreton Bay, the calving season appears to be compressed to about a three month period, mating-related combat is violent (Preen, 1989b) and herds are large. In tropical northern Australia, the calving season stretches over at least five months (Marsh et al., 1984a), mating may not associated with aggressive behaviour (Johannes and MacFarlane, 1991; Smith, 1987; but see Roughsey, 1971) and herds are generally small (Table 7.5).

Large herds of dugongs (≥ 100) have been confirmed from Moreton Bay, Shark Bay, the Arabian Gulf and the Starke River area in north Queensland (Table 7.5). The first three of these locations share one characteristic: they are all at the sub-tropical ends of the dugong's distribution (respectively 28°S, 26°S and 26°N).

Unlike tropical areas, each of these locations is characterised by water temperatures during winter that are apparently marginal for dugongs (Anderson, 1986; Preen, 1989a; section 2.2). The constraints imposed by the cold water temperatures have a major impact on the biology of dugongs in Moreton Bay. During winter, the dugongs alter their movement patterns to incorporate a regular migration to warmer offshore waters (section 5.4.2.2), but they still lose body condition (section 6.6.3.1). I have argued that it is the combination of a sub-optimal diet and the stresses imposed by the cold water that result in this loss of condition and that the dugongs attempt to counter these stresses by maximising the quality of their diet (section 6.6.3). This is achieved by a number of strategies, including 'cultivation' grazing.

'Cultivation' grazing occurs when large herds of dugongs forage intensively in an area, effecting a high level of seagrass removal over a large area. I have shown that in Moreton Bay, 'cultivation' grazing may allow the dugongs to improve the quality of their diet by one or more of the following: (1) converting the meadow to a lower seral stage composed of preferred and nutritionally superior seagrasses, (2) maintaining the meadow at a younger, actively growing stage, so the seagrasses contain more nitrogen and less fibre and (3) concentrating the regrowth vegetation into areas that can be efficiently cropped.

The nutritional benefits of these modifications to the seagrass meadows would maximise the fitness of individual dugongs. However, due to their mode of feeding, these benefits could only be achieved if the dugongs fed in large herds. These findings are in accord with McNaughton's (1984) hypothesis that the fitness benefits gained by individual animals, through increased foraging efficiency, could lead to the development of herding behaviour in ungulates.

If the benefits of 'cultivation' grazing can explain the tendency of dugongs in Moreton Bay to forage in large herds, why are these benefits not available to, or not important to dugongs in tropical areas, where herds are usually small? I suggest three, non-exclusive, possible explanations.

(i). Tropical dugongs do not have to contend with the same stresses.

On the basis of the seasonal behavioural changes observed in Moreton Bay and Shark Bay, combined with the distribution of dugongs in the Arabian Gulf and Shark Bay in relation to water temperature, it is apparent that dugongs are intolerant of water temperatures below about 18-19°C (Anderson, 1986; Marsh et al., 1991; Preen, 1989a; sections 5.4.5). Florida manatees cannot survive for long periods in water below 20°C (Irvine, 1983). In areas that are more tropical than Moreton Bay, water temperatures remain above 18° C during winter. Dugongs in those areas, therefore, do not have to contend with the physiological stress of cold water, nor the energetic demands of migration and fasting associated with the use of warm water refuges. Therefore, although tropical dugongs must tolerate some seasonal nutritional stresses, as suggested by the growth layers in their teeth (Lanyon, 1991; Marsh, 1980), the nutritional quality of their diet may not be as critical as it is in Moreton Bay. This suggestion is supported by the omnivory practised by dugongs in Moreton Bay, but not in northern Australia and Torres Strait (section 6.6.2.1). The fitness benefits that can accrue from feeding in large herds, therefore, may be less significant to tropical dugongs.

(ii). Different seagrasses in the tropics

In Moreton Bay, the effects of 'cultivation' grazing are particularly beneficial because of the nutritional differences between the climax species of seagrass (Z. capricorni broad), and the pioneer species (H. ovalis) that replaces it following intensive grazing disturbance. Z. capricorni is the least digestible seagrass in Moreton Bay, and it is the species least preferred by the dugongs. At the other extreme, H. ovalis is the most nutritious and most preferred species (section 6.6.2).

Z. capricorni is the dominant species of seagrass from Moreton Bay south to the Victorian border and Zostera species (most probably Z. capricorni; West et al., 1989) occurred in 28 of 30 major areas of seagrass along this coastline (28° S to 38° S; West et al., 1989). In tropical Queensland, however, Z. capricorni was found in only 3 of 29 major areas of seagrass between Cairns and Torres Strait (17° S to 10° S; Coles et al., 1987). Only 2 out of 65 dugongs from tropical Queensland had eaten Z. capricorni before their death (Marsh et al., 1982), while 40 of 48 faecal samples collected from dugongs in Moreton Bay contained Z. capricorni leaf (section 6.4.1.2). In contrast to Moreton Bay, Z. capricorni is not a significant feature of most tropical seagrass communities.

If a principal benefit of 'cultivation' grazing is the effective containment of seagrass meadows dominated by Z. capricorni, no such benefit would accrue in tropical areas. All other tropical species of seagrass analysed by Lanyon (1991) had lower fibre levels than Z. capricorni, so this species' unique nutritional status is not assumed by a different seagrass in the tropics.

(iii). Other sources of 'disturbance' in the tropics

'Cultivation' grazing improves the nutritional qualities of seagrass meadows in Moreton Bay because the grazing disturbance interrupts the succession of species, returning the community to a lower seral stage. In tropical areas, other types of disturbance, or other limiting factors, may achieve the same result, thus obviating the need for grazing by large herds.

Cyclones are one of the most prominent sources of disturbance in the tropics and may be major structuring forces in tropical seagrass systems (Poiner et al., 1989; Poiner et al, 1992). In northern Australia, an average of five cyclones cross the coast each year (Poiner, et al. 1989). The impact of cyclones on seagrass communities can be highly variable ranging from a barely detectable effect (Poiner et al., 1989; Thomas et al., 1960) to complete removal of all seagrass and even sediment from large areas (Birch and Birch, 1984; Poiner et al., 1989). Birch and Birch (1984) document the 10 year recovery of a tropical seagrass community decimated by a cyclone. The bay was first dominated by the pioneer species H. ovalis and Halophila ovata followed by H. uninervis with the eventual return to the C. serrulata dominated community.

Grazing by turtles may be another important form of seagrass disturbance in the tropics. Green turtles (Chelonia mydas) usually only crop the leaves of seagrasses, and do not disturb the rhizomes (Bjorndal, 1980; Lanyon et al., 1989), however, loggerhead turtles (Caretta caretta) can cause substantial damage. In Moreton Bay loggerheads create trenches in the seagrass beds as they forage for invertebrates in the sediments. These trenches can be over 8 m long, 1 m wide and 0.25 m deep (pers. obs.). Including the seagrasses within 1 m either side of the trench, which are smothered by excavated sediment, a single loggerhead turtle can disturb a substantial area of seagrass. The density of large turtles (principally greens and loggerheads, visible from an aerial survey altitude of 137 m) in tropical Queensland is three to four times greater than in Moreton Bay (Marsh and Saalfeld, 1990b). If a substantial proportion of these turtles are loggerheads, and if they feed in the manner observed in Moreton Bay, disturbance by turtles in the tropics could be significant.

In inter-tidal areas, frequent exposure of seagrass beds to intense sunlight during spring low tides during the day could interrupt the succession of seagrasses and maintain communities at low seral stages. Bridges et al. (1982) proposes this form of disturbance to explain the high diversity if inter-tidal seagrass beds in Torres Strait.

At the other extreme, the limited availability of sunlight may also account for the distribution of subtidal seagrasses in some areas. The depth limit of seagrasses is determined by light attenuation (Dennison, 1987; Duarte, 1991; Kenworthy and Haunert, 1991), and the waters of most inshore areas of tropical Queensland are noticeably more turbid than the waters of the East study area in Moreton Bay (G. E. Heinsohn and H. Marsh, pers. comm.). Hence, in those tropical areas, turbid water may act to limit the dominance of light demanding species of seagrass. Species of Halophila are among the most tolerant of low light levels (see Figure 1 in Duarte, 1991; Kenworthy et al., 1991), and hence, their relative abundance may be greater in turbid tropical waters than in clear water areas, such as the Moreton Bay study area.

The occasional disturbance of large areas by cyclones, regular disturbance of small areas by foraging turtles, disturbances to inter-tidal areas due to exposure, and light limitations in deeper water imposed by turbidity, may function to maintain a state of disclimax in a significant proportion of seagrass communities in the tropics. Under these circumstances, the relative abundance of the early seral stage species preferred by dugongs, may be enhanced to the point where dugong-induced damage is not required to ensure a good quality diet.

7.4.5.4. Dugong density

The herding of dugongs in Moreton Bay may also be a function of density. An estimated 95% of the population of dugongs in Moreton Bay can be found on the seagrass banks to the west of South Passage (section 5.2.2.3). This area contains approximately 35% of the area of seagrass in Moreton Bay (Hyland et al., 1989). On the basis of the aerial survey sightings, I estimate that about 81 km^2 of the seagrass banks in this area are used by the dugongs. A population of about 600 dugongs (section 5.4.1) therefore, translates to a density of approximately 7.4 dugongs/km^2. Due to a lack of comparative data collected on a similar scale, it is difficult to know if this is exceptional, although the size of the dugongs' home ranges provides some indirect evidence. On average, the home range of dugongs in Moreton Bay (64 km^2) was twice as large as the home range of four dugongs tracked in the Starke River area in tropical Queensland (30 km^2: dugongs D3-D6 Table 5.8). As the size of an individual's home range increases with the number of animals that share the space (and resources; Damuth, 1981), these data suggest that the density of dugongs in the East study area may be substantially greater than in the Starke area, which supports one of the largest known populations of dugongs. The proximity of the eastern banks to South Passage (and therefore to the winter warm-water refuge), may be responsible for concentrating the Moreton Bay population of dugongs in this area. If this is so, and if herding is density dependent, then unusually large herds may form. High densities of African elephants (Loxodonta africana) caused by a restriction in available habitat led to an increase in group size (Laws, 1970) and group size is also correlated with population density in Eastern grey kangaroos (Macropus giganteus; Taylor, 1982).

It is impossible to choose between these possible explanations of the herding of dugongs in Moreton Bay. Too little is known of their ecology. It is probable that there is no simple explanation and that a variety of factors, both known and unknown, are responsible for this behaviour. Ironically, the largest information gap concerns the ecology of dugongs in tropical areas (where the vast majority occur). This should now be redressed.

Table 7.1. Results of analyses of variance testing for yearly and seasonal differences in the 'typical' herd size and mean herd size of dugongs recorded during 28 aerial surveys of the East and West study areas in Moreton Bay.

	'Typical' herd size				Mean herd size			
Factor	df	MS	F	p	df	MS	F	p
Year[1]	1	15.1	0.00	0.9636	1	68.0	0.05	0.8213
Season[1 2]	3	4158.8	0.58	0.6316	3	546.6	0.41	0.7456
Yr*Season	2	769.4	0.11	0.8979	2	51.8	0.04	0.9619
Error	21	7111.2			1062	1331.9		
Total	27				1068			

[1] Fixed factors
[2] Year 1: winter, spring, summer, autumn; Year 2: winter, spring, summer

Table 7.2. Result of analysis of variance testing for yearly and seasonal differences in the proportion of calves in dugong herds counted during standard aerial surveys of the East and West study areas in Moreton Bay. Proportions were arcsine transformed.

Factor	df	MS	F	p
Year[1]	1	0.00071	0.45	0.5100
Season[1 2]	3	0.00290	1.83	0.1721
Yr*Season	2	0.00070	0.44	0.6490
Error	21	0.00158		
Total	27			

[1] Fixed factors
[2] Year 1: winter, spring, summer, autumn; Year 2: winter, spring, summer

Table 7.3. Results of analyses of variance comparing the proportion of calves, 'typical' herd size and mean herd size in different years and in two different periods relative to the period of calving. Calf proportions were arcsine transformed.

	Proportion of calves				'Typical' herd size				Mean herd size			
Factor	df	MS	F	p	df	MS	F	p	df	MS	F	p
Year[1]	1	0.0001	0.06	0.804	1	70	0.01	0.920	1	150	0.12	0.733
Period[1 2]	1	0.0010	0.57	0.456	1	19	0.00	0.960	1	82	0.06	0.801
Yr*Period	1	0.0001	0.08	0.780	1	1397	0.21	0.653	1	11	0.01	0.925
Error	24	0.0018			24	6716			1062	1290		
Total	27				27				1065			

[1] Fixed factors
[2] Post-calving period (December-March) and other months (April-November)

Table 7.4. Proportion of calves recorded during selected dugong surveys. Data is ordered by latitude within ranges of survey altitude. A range of values indicates results from different areas. All locations are in Australia, except the Arabian Gulf, eastern Red Sea and Manus (Papua New Guinea).

Latitude	Dugongs on which calf % based	% calves	Survey altitude (m)	Location	Date of survey (mo/yr)	Reference
28°S	28	7.7	137	Moreton Bay	7/88	Marsh et al., 1990
26°S	354	19.2	137	Shark Bay	7/89	Marsh et al., 1991
25-26°S	195	22.1	137	Hervey Bay-Tin Can Bay	7/88	Marsh et al., 1990
24-27°N	674[3]	12.9	152	Arabian Gulf	1/86	Preen, 1989a
24-27°N	215	15.3	152	Arabian Gulf	8-10/86	Preen, 1989a
24-27°N[1]	148	12.8	152	Arabian Gulf	1985-1987	Preen, 1989a
22°S	108	24.0	137	NW West Australia	7/89	Marsh et al., 1991
16-28°N	73	1.4	152	E Red Sea	6-8/87	Preen, 1989a
16-28°N	47	14.9	152	E Red Sea	6-8/87	Preen, 1989a
15-24°S	54-80	7.7-14.8	137	E Queensland	1986-1987	Marsh and Saalfeld, 1990a
12-15°S	75-270	10.4-16.3	137	NE Queensland	1984-1985	Marsh and Saalfeld, 1989
13-16°S	251	9.2	137	Northern Territiory	8/84	Bayliss and Freeland, 1989
13-16°S	184	12.5	137	Northern Territiory	2/85	Bayliss and Freeland, 1989
10°S	311	13.6	137	Torres Strait	11/87	Marsh and Saalfeld, 1988
10°S	161	14.3	137	Torres Strait	3/88	Marsh and Saalfeld, 1988
14-15°S	224	13.3	137+275	Cape Flattery Cape Melville	11/84	Marsh, 1985
13°S	133	3.0	136+272	Northern Territory	12/83	Bayliss, 1986
28°S[1]	10,326	10.1	274	Moreton Bay	1988-1990	This study
28°S	210	6.7	275-300	Moreton Bay	5/77	Heinsohn, 1977
28°S	307	5.5	275-300	Moreton Bay	8/79	Heinsohn & Marsh, 1979
26°S	99-445[2]	8.3-12.3	275	Shark Bay	7/79	Anderson, 1982a
25-26°S	156	7.1	275-300	Hervey Bay-Tin Can Bay	8/79	Heinsohn & Marsh, 1979
22-24°S	200	1.0	275-300	Rodds Bay-Shoalwater Bay	8/79	Heinsohn & Marsh, 1979

Latitude	Dugongs on which calf % based	% calves	Survey altitude (m)	Location	Date of survey (mo/yr)	Reference
19-22°S	26	2.3	275-300	Townsville-Broadsound	7/78	Heinsohn & Marsh, 1978
18-19°S[1]	395	4.5	275-300	Townsville	1974	Heinsohn et al., 1976 & Heinsohn, 1975
18-19°S	31	3.2	275-300	Townsville	1/78	Heinsohn & Marsh, 1978
18-19°S	44	2.3	275-300	Townsville	8/78	Heinsohn & Marsh, 1978
18-19°S	23	4.3	275-300	Townsville	11/78	Heinsohn & Marsh, 1978
18-19°S	29	6.9	275-300	Townsville	11/80	Heinsohn & Marsh, 1981
14-15°S	171	2.9	275-300	Cape Flattery-PCB[4]	11/74	Heinsohn et al., 1976
14-15°S	236	8.1	275-300	Cooktown-PCB	7/80	Heinsohn & Marsh, 1981
10-26°S	629	4.6	275	Most Queensland	3-4/75	Ligon, 1976
2°S[1]	157	10.2	300	Manus, PNG	1978-1980	Hudson, 1981

[1] Pooled results of repeated surveys
[2] Calf counts from smaller groups not included
[3] Calf count derived from photos of parts of the herd (n = 8, SE = 3.1)
[4] Princess Charlotte Bay

Table 7.5. Information on the size of dugong herds. Data has been extracted from aerial survey reports that recorded a total of at least 30 sighted dugongs. Data are arranged by decreasing latitude within each of two survey types. Shoreline surveys are typically flown at an altitude of 274-300 m and transect width is not restricted. Line-transect surveys are usually flown at an altitude of 137-152 m and have a fixed transect width. A range of values indicates results from different areas or survey blocks. Some data were not available (NA). All locations are in Australia, except the Arabian Gulf, eastern Red Sea and Manus (Papua New Guinea).

Latitude	Total dugongs seen	Number of groups	Mean herd size	Maximum herd size	Survey altitude (m)	Location	Date of survey (mo/yr)	Reference
Shoreline surveys								
28°S[1]	10,326	1,069	9.7	459	274	Moreton Bay	1988-1990	This study
28°S	210	22	9.5	66	275-300	Moreton Bay	5/77	Heinsohn, 1977
28°S	307	49	6.3	100	275-300	Moreton Bay	8/79	Heinsohn & Marsh, 1979
26°S	1,537	400	3.8	134	275	Shark Bay	7/79	Anderson, 1982a
26°S[1]	590	77	7.7	68	275-300	Shark Bay	6/78, 4/79	Prince et al., 1981
25-26°S	156	65	2.4	50	275-300	Hervey Bay-Tin Can Bay	8/70	Heinsohn & Marsh, 1979
24-27°N[1]	148	683	2.2	25	152	Arabian Gulf	1985-1987	Preen, 1989a
22-24°S	200	112	1.78	17	275-300	Rodds Bay-Shoalwater Bay	8/79	Heinsohn & Marsh, 1979
20-22°S[1]	223	46	4.8	60	275-300	NW West Australia	2/77, 7/78	Prince et al., 1981
16-28°N	47	31	1.5	6	152	E Red Sea	6-8/87	Preen, 1989a
22°S	117	NA	NA	43	275-300	Shoalwater Bay	6/75	Heinsohn, 1976
22°S	213	NA	NA	100[3]	275-300	Shoalwater Bay	10/75	Heinsohn, 1976
18-19°S	48	20	2.8	7	275-300	Townsville	9/74	Heinsohn, 1975 & Heinsohn et al., 1976
18-19°S	74	24	3.1	13	275-300	Townsville	11/74	Heinsohn, 1975 & Heinsohn et al., 1976
18-19°S	89	22	4.1	24	275-300	Townsville	8/75	Heinsohn, 1975
18-19°S	98			22	275-300	Townsville	6/77	Heinsohn, 1977
18-19°S	31	17	1.8	10	275-300	Townsville	1/78	Heinsohn & Marsh, 1978
18-19°S	44	29	1.5	4	275-300	Townsville	8/78	Heinsohn & Marsh, 1978
17°S	59	27	2.2	10	275-300	Wellesley Islands	4/77	Marsh et al., 1981 & Heinsohn, 1977
17°S	213	70	3.0	<30	275-300	Wellesley Islands	4/77	Marsh et al., 1981 & Heinsohn, 1977
17°S	374	213	1.8	<20	275-300	Wellesley Islands	11/77	Marsh et al., 1981 & Heinsohn, 1977
10-19°S	480	80	1.8[4]	182	275-300	E Cape York	11/78	Heinsohn and Marsh, 1978
10-17°S	96	64	1.5	8	275-300	W Cape York	11/78	Heinsohn and Marsh, 1978
14-15°S	171	47	3.6	67	275-300	Cape Flattery-PCB[5]	11/74	Heinsohn et al., 1976
14-15°S	695	55	2.4[6]	<100	275-300	Cape Flattery-PCB	6/78	Heinsohn & Marsh, 1978

Latitude	Total dugongs seen	Number of groups	Mean herd size	Maximum herd size	Survey altitude (m)	Location	Date of survey (mo/yr)	Reference
14-15°S	236	86	2.7	55	275-300	Cooktown-PCB	7/80	Heinsohn & Marsh, 1981
14-15°S	78	42	1.9	33	275	Cape Flattery Cape Melville	11/84	Marsh, 1985
12-16°S	486[7]	111	4.4	27	275-300	Northern Territiory	11/77	Elliott et al., 1981 and Heinsohn, 1977
10°S	60	19	3.2	13	61-152	Torres Strait	12/75	Heinsohn, 1976
2°S[1]	157	85	1.8	25	300	Manus, PNG	1978-80	Hudson, 1981
Line-transect surveys								
28°S	168	20	8.4	140	137	Moreton Bay	7/88	Marsh et al., 1990
25-26°S	217	77	2.8	22	137	Hervey Bay-Tin Can Bay	7/88	Marsh et al., 1990
24-27°N	686	12	57.1	674[2]	152	Arabian Gulf	1/86	Preen, 1989a
24-27°N	215	143	1.5	52	152	Arabian Gulf	8-10/86	Preen, 1989a
26°S	437	NA	NA	>100[8]	137	Shark Bay	7/89	Marsh et al., 1991
16-28°N	73	51	1.4	5	152	E Red Sea	6-8/87	Preen, 1989a
15-24°S	NA	NA	1.3-1.7	10	137	E Queensland	1986-1987	Marsh and Saalfeld, 1990a
12-15°S	NA	NA	1.5-1.6	20	137	NE Queensland	1984-1985	Marsh and Saalfeld, 1989
15°S	95	63	1.5	8	137	Cape Flattery Cape Melville	11/84	Marsh, 1985
13-16°S	251	152	1.6	14	137	Northern Territiory	8/84	Bayliss and Freeland, 1989
13-16°S	184	112	1.6	15	137	Northern Territiory	2/85	Bayliss and Freeland, 1989
13°S	133	111	1.2	6	136-272	Northern Territory	12/83	Bayliss, 1986
10°S	311	224	1.39	5	137	Torres Strait	11/87	Marsh and Saalfeld, 1988
10°S	311	224	1.39	5	137	Torres Strait	11/87	Marsh and Saalfeld, 1988

[1] Pooled results of repeated surveys
[2] Two sub-groups: 577 and 97
[3] Dispersed along 5 km of coastline
[4] 310 dugongs seen along 23 km of coastline in groups of 1-182. Number of groups and mean group size estimates exclude this 'group' of 310 and another 'group' of 72 that was composed of smaller groups.
[5] Princess Charlotte Bay
[6] 564 dugong seen along 15 km of coastline in groups of 1-<100. Number of groups and mean group size estimates exclude this 'group' of 564.
[7] A total of 557 dugongs were seen, but details of the group sizes in a count of 71 dugongs from one area were not recorded.
[8] Very diffuse.

Figure 7.1. Relative frequency distribution of herd sizes of dugongs in the East and West study areas during different seasons and years.

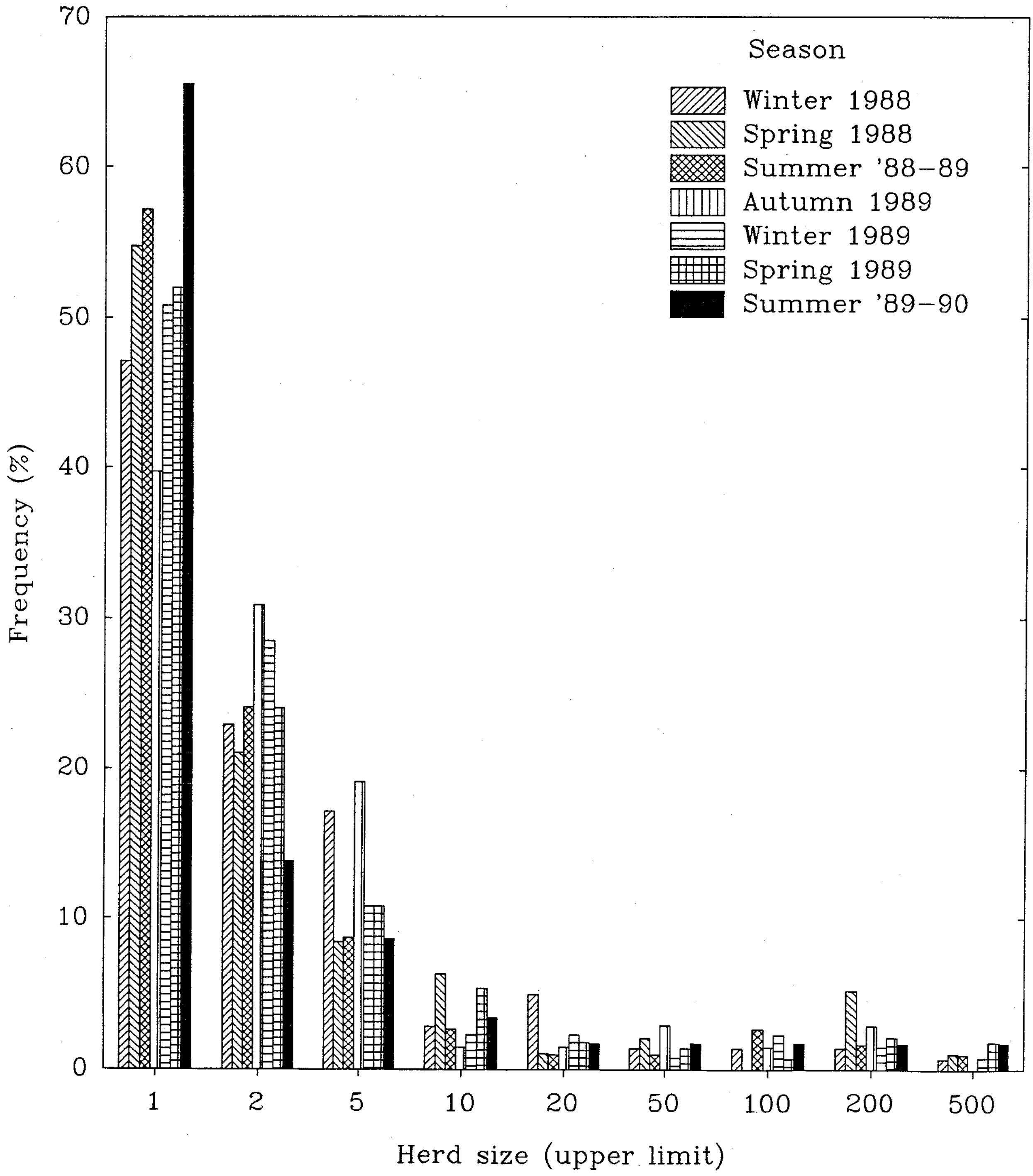

Figure 7.2. Cummulative percentage of dugong herds (□) in 26 size classes (upper limit plotted) and the cummulative proportion of dugongs in herds of different sizes (○). Data from 28 aerial surveys of the East and West study areas. n = 1,069 herds and 10,326 dugongs.

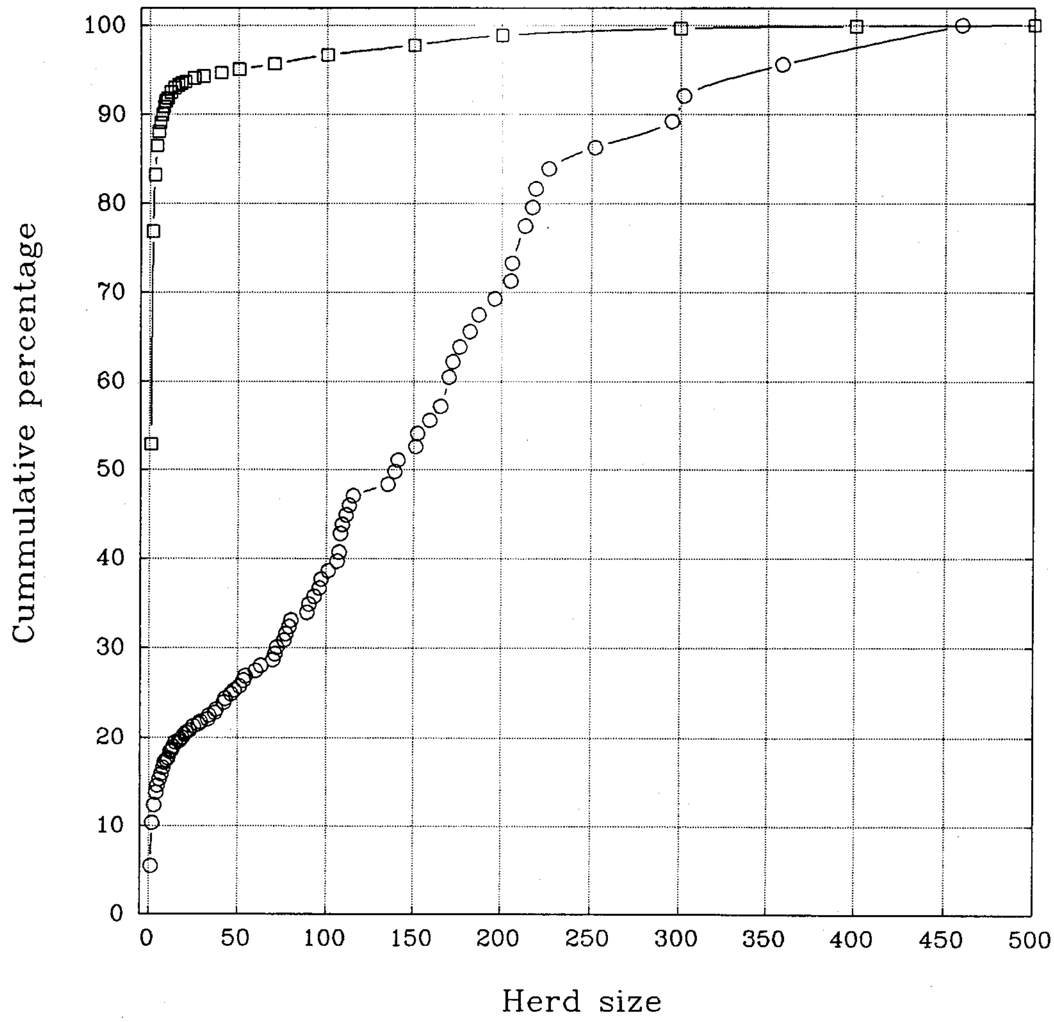

Figure 7.3. Total number of dugongs seen during each of 28 aerial surveys of the study areas, and the maximum, 'typical' and mean sizes of herds and the proportions of calves recorded.