

# Morphological differences between two closely related sea urchin species, *Strongylocentrotus droebachiensis* and *S. pallidus*, in northern Norway (Echinodermata, Echinoidea)

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Using material from a mixed population in northern Norway, it is shown that the two sea urchin taxa *Strongylocentrotus droebachiensis* (O.F. Muller) and *S. pallidus* (G.O. Sars) are independent, although closely related species, that are fairly easy to tell apart also by morphological criteria.

In this mixed population there is a significant difference in relative lantern size, with *S. pallidus* having much bigger lanterns. The difference is especially pronounced in large specimens.

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## INTRODUCTION

The sea urchin family Strongylocentrotidae has its centre of distribution in the northern Pacific Ocean, where all 10 recent species occur (Jensen 1974). Two species, *Strongylocentrotus droebachiensis* (O.F. Muller) and *S. pallidus* (G.O. Sars) are additionally found throughout the northern part of the Atlantic Ocean, the Norwegian Sea and the low Arctic; both species have originally been described from Norwegian waters. Although this pattern of distribution strongly indicates that the two species have existed as separate taxa for a long time, they are morphologically and biologically quite similar, and Sars' (1871) description of *S. pallidus* as a species specifically different from *S. droebachiensis* was not generally accepted.

In his monumental and vastly influential 'Monograph of the Echinoidea' Mortensen (1943) dismissed *S. pallidus* as a mere colour-variety of the very variable *S. droebachiensis*, of no taxonomic value whatsoever. He did, on the other hand, recognize the northern Pacific taxa *S. sachalinicus* Döderlein, 1906 and, provisionally, *S. echinoicus* Agassiz & Clark, 1907, as specifically distinct. Both are now considered synonyms of *S. pallidus* (Jensen 1974).

Later work, primarily by experimental biologists (Vasseur 1951, 1952, Swan 1953, 1962, Hagström & Lønning 1967) has made clear that *S. droebachiensis* and *S. pallidus* are distinct, though closely related, species that occur sympatrically over the

entire northern Atlantic and Pacific, albeit with some differences in horizontal and vertical distribution. Studies of skeletal characters (Jensen 1974), reproductive cycles (Falk-Petersen & Lønning 1983) and egg, embryo and larval characters (Hagström & Lønning 1976, Strathmann 1979, Falk-Petersen 1983, Lønning & Vader, in prep.) have confirmed the specific distinctness of the two species. Several authors have, nevertheless, continued to combine the two sub nom. *S. droebachiensis* (e.g. Brun 1964, Skjæveland 1973, Vadas 1977).

The occurrence of two closely related sympatric *Strongylocentrotus* species is of considerable ecological interest, especially since the two species also have overlapping spawning seasons (Falk-Petersen & Lønning 1983), cross-fertilization is possible in the laboratory (Hagström & Lønning 1967) and the resulting hybrids are fertile (Strathmann 1981). As a basis for comparative studies of the biology of the two species and of geographic intra- and interspecific variations in morphology and biology (Hagedal Pedersen 1981, Lønning & Vader, in prep., Vader et al. in prep.), it was thought useful to collect further data on the morphological differences between *S. droebachiensis* and *S. pallidus* from an area where the two occur together, so that habitat-induced phenotypical differences can be ruled out. The present work was carried out at Tromsø in northern Norway, the site of Vasseur's pioneering studies (Vasseur 1951, 1952); it formed part of the second author's thesis (Hagedal Pedersen 1981).

## MATERIAL AND METHODS

Sea urchins were collected by SCUBA-diving or dredging at 5–20 m depth in one of the shallow sounds around the island of Tromsø (69° 38'N, 19° 56'E), that constitute the sill of Balsfjorden in northern Norway. The topography and hydrography of the collecting station have been described by Hagedal Pedersen (1981): water temperatures vary from c. 1°C in March–April to ca. 9°C in August–September, and because of strong turbulent tidal currents are the same at all depths. The substrate consists mainly of a near-vertical cliff with some Laminariaceae and many calcareous algae.

The collected sea urchins were brought to the laboratory alive. Specimens were initially sorted into species by habitus and colour of test and spines, and this identification was then checked using the characters of the tridentate pedicellariae (Vasseur 1951, Jensen 1974). Diameter and height of the tests were measured to the nearest mm using vernier calipers appressed as closely as possible, while volume was measured by water displacement in a beaker glass. For measurement of spine length the 5 longest primary spines from 2 of the 5 ambulacral areas were measured. Similarly, the number of pore pairs was counted from 10 ambulacral plates. Aristotle's lantern was dissected out and weighed, after overnight drying, to the nearest 0.01 g.

Age determination was by counting annual rings in the interambulacral plates after heating and treatment in a xylene solution, as described by Jensen (1969). The method is technically difficult, time consuming and dangerous to the health; for this reason only a limited number of specimens have

been aged. Volume rather than age is used as a parameter for most comparisons in this paper (see Hagedal Pedersen 1981 for comparisons involving aged specimens).

## RESULTS

In the Tromsø area *Strongylocentrotus droebachiensis* and *S. pallidus* are easily identified in the field. *S. droebachiensis* is dark purple with long spines, while *S. pallidus* is light red or pale green with shorter spines. The difference in colour is even more obvious under water. When checked against the form of the tridentate pedicellariae, the field identifications were invariably found to be correct.

Although *S. pallidus* specimens often gives the impression of being taller at any given diameter there is in reality no significant difference in the width-height proportions of the two species (Fig. 1). The misleading impression is probably caused by the somewhat different shape of the test: *S. pallidus* usually has its greatest diameter in the lower half of the test, *S. droebachiensis* near the middle. Also, *S. droebachiensis* has longer spines.

There is no significant difference in growth rate between the two species (Fig. 2); both reach a maximum size of ca. 100 ml. volume at an age of 8–9 years.

*S. droebachiensis* has significantly longer primary spines than *S. pallidus* at any age (Fig. 3). There were no intraspecific differences in spine-length, when specimens from different substrates are compared (Hagedal Pedersen 1981). The often slightly «unkempt» appearance of *S. droebachiensis*

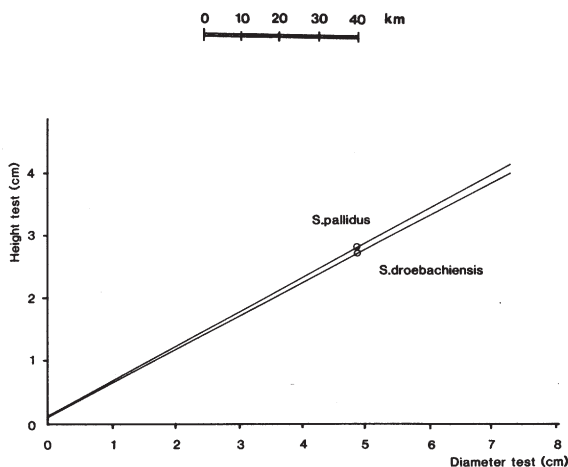


Fig. 1. Relation between test width and height in *S. droebachiensis* and *S. pallidus* from Tromsø (N=20).

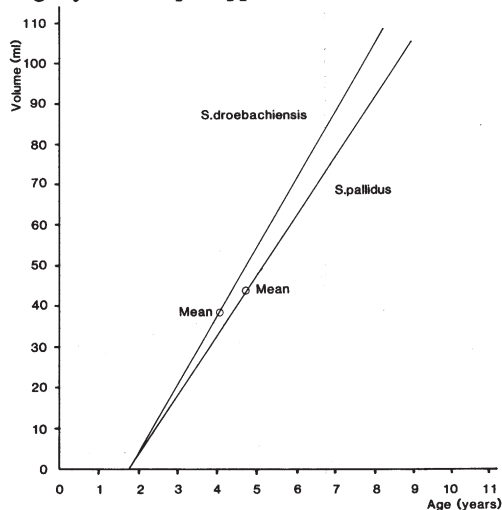


Fig. 2. Relation between age and size in *S. droebachiensis* and *S. pallidus* from Tromsø (N=50).

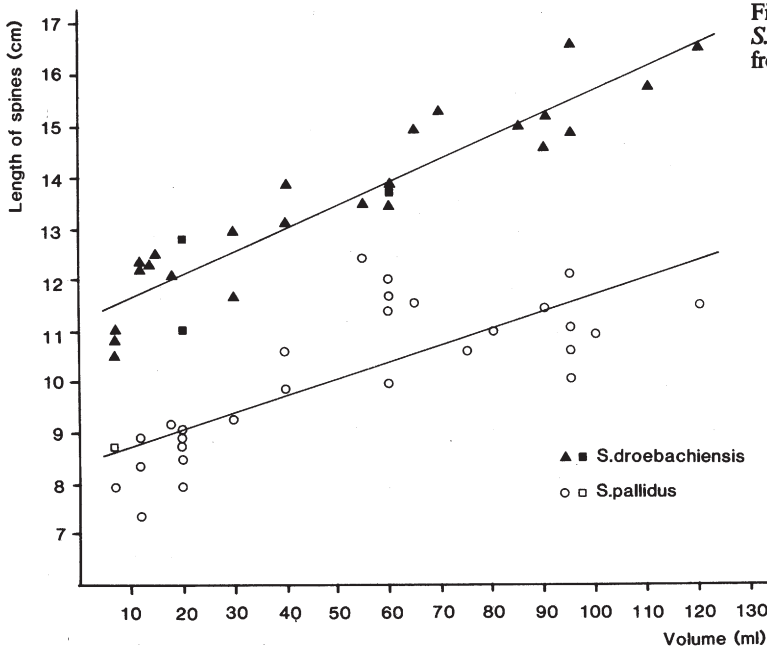


Fig. 3. Length of primary spines in *S. droebachiensis* and *S. pallidus* from Tromsø.

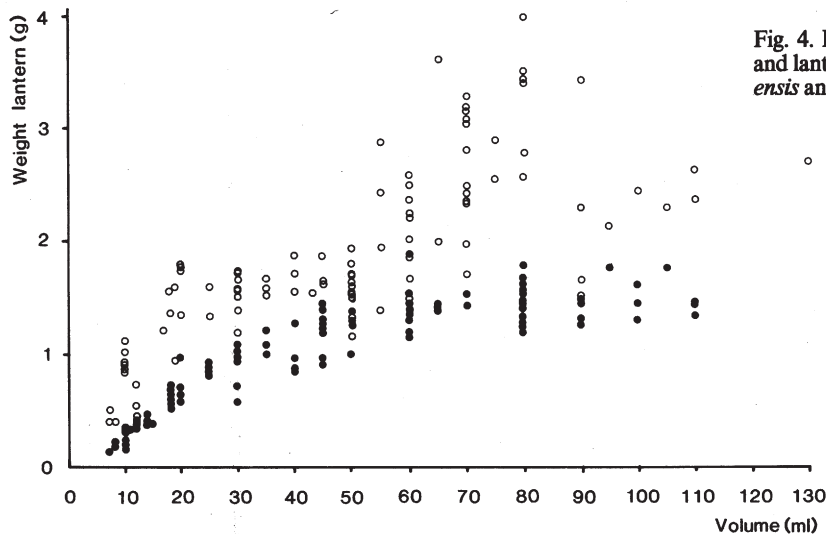


Fig. 4. Relation between total size and lantern weight in *S. droebachiensis* and *S. pallidus* from Tromsø.

*sis* compared to *S. pallidus* results from the much more uneven spine length (Fig. 1); because of spine repairs this character is difficult to quantify.

A very clearcut difference exists in the relative size of Aristotle's lantern in the two species (Fig. 4). *S. pallidus* has a significantly bigger lantern at any given size; the difference becomes especially pronounced in large specimens. The reason for this appears to be that absolute lantern size ceases to increase in *S. droebachiensis* at a volume of 50–60 ml, i.e.

an age of 5–6 years (Fig. 2). In *S. pallidus*, on the other hand, lantern weights increase at least to a volume of 70–80 ml, i.e. an age of 7–8 years. There is considerable individual variation in lantern size, especially among large *S. pallidus*, but no seasonal variation.

Data on the colour of the test, the number of radial stripes in juvenile specimens, the number of pore-pairs, the size of the globiferous pedicellariae and the form of the tridentate pedicellariae have

also been collected during this study (Hagedal Pedersen 1981); these data agreed in all particulars with those of earlier workers (Vasseur 1951, 1952, Hagström & Lönning 1967, Jensen 1974) and will not be repeated here. Differences noted by Vasseur (1951, 1952) in the form of the globiferous pedicellariae, the madreporite plate, and Aristotle's lantern were found to be non-diagnostic, because of large intraspecific variability.

Data on bathymetric distribution and behavioral differences between the two species (Hagedal Pedersen 1981) will be treated in a separate paper.

## DISCUSSION

In the Tromsø area, *Strongylocentrotus droebachiensis* and *S. pallidus* are easy to distinguish in the field, and there is good agreement between the field characters (colour, spine length), and the diagnostic form of the tridentate pedicellariae, as noted earlier by Vasseur (1951, 1952) and Hagström and Lönning (1967). Most of the diagnostic morphological characters noted by Sars (1871), Vasseur (1951, 1952) and Jensen (1974) could also be confirmed and put on a firmer quantitative basis. Together with the physiological (Vasseur 1951, 1952, Hagström & Lönning), embryological (Hagström & Lönning 1967, 1976, Falk-Petersen 1983, Lönning & Vader in prep.) and biological (Vasseur 1951, Hagedal Pedersen 1981, Falk-Petersen & Lönning 1983, Vader et al. in prep.) evidence these make it clear that *S. droebachiensis* and *S. pallidus* behave as completely independent biological species in the Tromsø area, without any signs of introgression. Morphologically intermediate specimens (cf. Vasseur 1952) have not been found: hybrids may be easily overlooked, however, as they superficially strongly resemble the maternal parent species (Strathmann 1981).

Both *Strongylocentrotus* species show considerable geographic variation in characters such as test colour (Vasseur 1952, Jensen 1974), lantern size (Vasseur 1952) and egg diameter (Hagström & Lönning 1967). This variation makes identification of the two species less easy in both south Norwegian (Vasseur 1952, Hagström & Lönning 1967) and arctic populations; it will be the subject of a separate paper. As first noted by Vasseur (1951), the lantern of *S. pallidus* is relatively much heavier than that of *S. droebachiensis* in specimens from the Tromsø area. Vasseur's data (from a locality a few km's from the present one) are in complete agreement with ours for *S. droebachiensis*, and in the great individual variability of lantern size in medium and large *S. pallidus*, but his population shows a so-

ewhat earlier cessation of lantern growth in *S. pallidus*.

Relative lantern weight has been shown to vary geographically (Vasseur 1952, Vader et al., in prep.) and locally (Hagström & Lönning 1964 for *Echinus esculentus*, Ebert 1980 for *Strongylocentrotus purpuratus* and *Diadema setosum*, Black et al. 1982 for *Echinometra mathaei*), but usually not seasonally (Fuji 1969 for *Strongylocentrotus intermedius*). Lantern size is often negatively correlated with food availability (Ebert 1980, Black et al. 1982), with sea urchins with large lanterns being more efficient grazers (Black et al. 1984).

In the present study the two species occurred together in about equal numbers, and different food availability can only result from intraspecific competition. There is little evidence of direct competition for food between sea urchin species (cf. Duggins 1981), although Strathmann (1979) has hinted at the existence of such competition, with *S. droebachiensis* the dominant species. There is also a difference in microdistribution between the two species, with *S. droebachiensis* tending toward a clumped distribution and *S. pallidus* more evenly spaced (Hagedal Pedersen 1981).

In how far direct or indirect competition for food or favourable sites or different food preferences may result in unequal availability of food for the two sea urchin species, can be ascertained by field and laboratory observations and manipulations along the lines pioneered by Black et al. (1984).

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