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INVITED REVIEW

Goatfishes (Mullidae) as indicators in tropical and temperate coastal habitat monitoring and management

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Abstract

This review investigates if goatfishes qualify as habitat indicators and play a role as key species for use in coastal ecosystem monitoring and management, emphasizing major gaps of knowledge in goatfish ecology and systematics. Currently, 66 species of goatfishes are known, the family occurring widely in tropical, subtropical and temperate habitats from the upper littoral down to the upper slope. Studies of goatfish occurrence and abundance in natural habitats have documented general preferences for sand-associated bottoms after post-larval settlement that goes hand in hand with the development of the characteristic barbels. Species, populations and later life-history stages may, however, differ significantly from each other in habitat use. Some species are more restricted to hard bottoms, others separate mainly by depth. Goatfishes respond to human-induced factors such as fisheries and habitat modification, as reflected by abundance, size, or weight changes, or changes in their distributional ranges. Temperature increase may lead to increased reproductive or growth rates and longer warming periods may induce goatfishes to migrate to higher latitudes, as exemplified by striped red mullet (*Mullus surmuletus*) in the North Sea. Isolated occurrences of this species in the Norwegian Sea at 60°N have been documented. Goatfishes may act as allochthonous ecosystem engineers through their vigorous foraging behaviour with barbels and mouth, which leads to the stirring-up of sediments and associated detritus particles high into the water column. Goatfishes play a key role in the formation of multi-species foraging associations as nuclear species that are followed by many other species. The role of goatfishes in food webs has been rarely evaluated and the many interactions goatfishes may be involved in have not yet been sufficiently considered. There is also a considerable lack of basic systematic and taxonomic knowledge, new species still being described and intraspecific morphological variation and genetic differentiation requiring more detailed studies. Goatfishes clearly deserve more attention in future coastal habitat exploration, monitoring and management efforts.

Key words: *Fisheries, key species, multi-species foraging, resuspension, systematics, temperature*

Introduction

Coastal waters are highly structured, covering a large variety of different bottom types that are inhabited by a diverse assemblage of organisms. Many of these habitats are still insufficiently known and require continued effort to sample, describe and register all species. However, due to increasing signs of human-induced local and global impacts (e.g. Cohen et al. 1997; Gommes et al. 1998; Phillippart 2007), there is also a pressing need to study further coastal organisms to understand their ecological role and function and to evaluate their potential use as indicators and/or key species for coastal ecosystem monitoring and management.

Indicators are here defined as a subset of organisms that strongly and transparently respond to distinct natural or human-induced factors or changes. 'Strongly and transparently' shall signify that observed responses should be directly related to distinct factors, relatively easy to measure and, hence, cost- and time-effective. The measuring of such responses can be based on occurrence and distribution patterns, local abundance, weight, size, behaviour or physiology (Nicholls 2002). Indicators should be relatively abundant and widespread, easy to sample and tolerant to a wide variety of environmental conditions.

Key species interact tightly with an entire assemblage and are able to modify it directly or indirectly. Some key species act as 'ecosystem engineers', as they physically change the environment, either by themselves or by manipulating distinct habitat features. Due to their interactive role, key species provide important information on ecosystem processes and,

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hence, can also be used as indicators of ecosystem integrity and state.

Most parsimonious, time- and cost-effective ecosystem monitoring and management may be achieved by using groups of easily accessible and widely distributed species that to some extent combine the features of indicator and key species (Nicholls 2002). Because these species will allow essential information to be obtained about distinct habitat features as well as about an overall assemblage within a certain area, they would be 'ecosystem indicators' in a very integrative way.

This study highlights the goatfishes, family Mullidae, as a group of mainly coastal organisms that have a high value for ecosystem monitoring and management, but also require intensified systematic and ecological research. Goatfishes are characterized by a pair of typical chin barbels that are very efficient tools for food search and location (Figure 1). This family comprises 66 species (Table I) that are distributed worldwide in tropical, subtropical and temperate habitats between the upper littoral and the upper slope.

Goatfishes are relatively common and of high economic importance in many coastal areas. This study investigates if goatfishes qualify as coastal habitat indicators and if they may also play a role as key species in coastal assemblages. Gaps in the knowledge in goatfish ecology and basic systematics are pointed out to stimulate further research.

Goatfishes as habitat indicators

In the last few years, considerable research on coastal fishes has been carried out to examine the effects of both naturally varying factors and human-induced modifications on habitat utilization at different scales (e.g. Horn et al. 1999; Hart & Reynolds 2002; Sale 2006). Goatfishes have been increasingly considered in such kinds of study, either jointly with other fish taxa or as the major study subjects. The following overview is based mainly on quantitative, comparative data from recent research on goatfishes. The first section deals with goatfishes as indicators of natural habitat followed by studies of the impact of fisheries and human-induced habitat modification. The final section deals with temperature and climate change. The overview tables (Tables II–V) follow the same structure, listing the species, area, major factors and parameters, specific observations and the results of the respective investigation(s), and the literature source(s).

Natural habitat

Goatfishes occur in a broad range of habitats, mostly close to or near the bottom of the littoral. However, some species may be found down to depths of 500 m (e.g. Golani 2001) and surface-dwelling goatfish larvae have sometimes been found drifting in the outer shelf (Hernandez et al. 2003) or in oceanic waters (Deudero 2002). Most goatfish species shift

Figure 1. Bicolour goatfish, *Parupeneus barberinoides*, searching for prey with barbels (top) and mouth (bottom). Note the different degrees of penetration and sediment disturbance. A full behavioural sequence starting with barbel search and ending with mouth search deep in the sediment is shown in a supplementary video clip available at: http://www.informaworld.com/mpp/uploads/goatfish_food_search_video.avi Both the photographs and the video clip were made in the Okinawa Churaumi Aquarium, Japan, February 2007 by the author.

Table I. The 66 species of the family Mullidae, as of June 2007 (Randall 2004; Randall & Kulbicki 2006; Froese & Pauly 2007).

Mulloidichthys dentatus (Gill, 1862)	*Parupeneus insularis* Randall & Myers, 2002	*Upeneus asymmetricus* Lachner, 1954
Mulloidichthys flavolineatus (Lacepède, 1801)	*Parupeneus jansenii* (Bleeker, 1856)	*Upeneus australiae* Kim & Nakaya, 2002
Mulloidichthys martinicus (Cuvier in Cuvier & Valenciennes, 1829)	*Parupeneus louise* Randall, 2004	*Upeneus crosnieri* Fourmanoir & Guézé, 1967
Mulloidichthys mimicus Randall & Guézé, 1980	*Parupeneus macronemus* (Lacepède, 1801)	*Upeneus davidaromi* Golani, 2001
Mulloidichthys pfluegeri (Steindachner, 1900)	*Parupeneus margaritatus* Randall & Guézé, 1984	*Upeneus doriae* (Günther, 1869)
Mulloidichthys vanicolensis (Valenciennes in Cuvier & Valenciennes, 1831)	*Parupeneus moffitti* Randall & Myer, 1993	*Upeneus filifer* (Ogilby, 1910)
Mullus argentinae Hubbs & Marini, 1933	*Parupeneus multifasciatus* (Quoy & Gaimard, 1825)	*Upeneus francisi* Randall & Guézé, 1992
Mullus auratus Jordan & Gilbert, 1882	*Parupeneus orientalis* (Fowler, 1933)	*Upeneus guttatus* (Day, 1868)
Mullus barbatus Linnaeus, 1758 (two subspecies)	*Parupeneus pleurostigma* (Bennett, 1831)	*Upeneus japonicus* (Houttuyn, 1782)
Mullus surmuletus Linnaeus, 1758	*Parupeneus porphyreus* (Jenkins, 1903)	*Upeneus luzonius* Jordan & Seale, 1907
Parupeneus barberinoides (Bleeker, 1852)	*Parupeneus posteli* Fourmanoir & Guézé, 1967	*Upeneus mascareinsis* Fourmanoir & Guézé, 1967
Parupeneus barberinus (Lacepède, 1801)	*Parupeneus procerigena* Kim & Amaoka, 2001	*Upeneus moluccensis* (Bleeker, 1855)
Parupeneus biaculeatus (Richardson, 1846)	*Parupeneus rubescens* (Lacepède, 1801)	*Upeneus mouthami* Randall & Kulbiski, 2006
Parupeneus chrysonemus (Jordan & Evermann, 1903)	*Parupeneus spilurus* (Bleeker, 1854)	*Upeneus parvus* Poey, 1852
Parupeneus chrysopleuron (Temminck & Schlegel, 1843)	*Parupeneus trifasciatus* (Lacepède, 1801)	*Upeneus pori* Ben-Tuvia & Golani, 1989
Parupeneus ciliatus (Lacepède, 1802)	*Pseudupeneus grandisquamis* (Gill, 1863)	*Upeneus quadrilineatus* Cheng & Wang, 1963
Parupeneus crassilabris (Valenciennes in Cuvier & Valenciennes, 1831)	*Pseudupeneus maculatus* (Bloch, 1793)	*Upeneus subvittatus* (Temminck & Schlegel, 1843)
Parupeneus cyclostomus (Lacepède, 1801)	*Pseudupeneus prayensis* (Cuvier in Cuvier & Valenciennes, 1829)	*Upeneus sulphureus* Cuvier, 1829
Parupeneus diagonalis Randall, 2004	*Upeneichthys lineatus* (Bloch & Schneider, 1801)	*Upeneus sundaicus* (Bleeker, 1855)
Parupeneus forsskali (Fourmanoir & Guézé, 1976)	*Upeneichthys stotti* Hutchins, 1990	*Upeneus taeniopterus* Cuvier in Cuvier & Valenciennes, 1829
Parupeneus heptacanthus (Lacepède, 1802)	*Upeneichthys vlamingii* (Cuvier in Cuvier & Valenciennes, 1829)	*Upeneus tragula* Richardson, 1846
Parupeneus indicus (Shaw, 1803)	*Upeneus arge* Jordan & Evermann, 1903	*Upeneus vittatus* (Forsskål, 1775)

to bottom life soon after metamorphosis, coinciding with barbel development (McCormick 1993) and changes in eye structure (Shand 1997). However, some species may remain in the open water as juveniles (McCormick & Milicich 1993) or feed on plankton even during later ontogenetic stages (Krajewski & Bonaldo 2006).

Studies on goatfish habitat use have considered depth as well as various bottom types, including hard and soft bottoms, open sandy areas and those overgrown with vegetation (Table II). Clear preferences for distinct habitat types, but also differences among species and size/age classes, have been reported. Goatfishes are most frequently found on sandy bottoms adjacent to hard bottoms, including coral reefs. Apart from daily short-distance movements within and among foraging and resting sites (Holland et al. 1993; Meyer et al. 2000), they may also show seasonal migrations, in particular during the reproductive period, leading to the formation of spawning aggregations (Colin & Clavijo 1978; Lobel 1978; Thresher 1984; Colin 1996; Machias & Labropoulou 2002; Claydon 2004).

Juvenile goatfishes are often encountered on soft bottoms, in seagrass beds or mangroves, and at different depths than adults, reflecting both horizontal and vertical ontogenetic habitat shifts (Table II). Serving as recruitment habitats, seagrass habitats may contribute positively to adult goatfish abundance in adjacent areas (Dorenbosch et al. 2005). Ontogenetic habitat shifts may also occur during later life history and coincide with changes in foraging mode, social behaviour and the formation of multi-species associations (Uiblein 1991; Figure 2).

There are marked differences among goatfish species with respect to preferred habitat type and depth (Table II). For instance, the red mullet, *Mullus barbatus*, and the striped red mullet, *M. surmuletus*, show clear differences in distribution and abundance, with the latter occurring more on hard bottoms and shallower (Lombarte et al. 2000).

Table II. Goatfish species as indicators of natural habitat.

Species	Study area	Major factor(s)	Parameter(s)	Specific observations	Source
Mulloidichthys flavolineatus	Western Indian Ocean	Sheltered reef fringing sand bank	Occurrence, abundance	Site-restricted occurrence, high abundance	Garpe & Öhman (2003)
Mulloidichthys flavolineatus, seven *Parupeneus* species	Southwest Pacific	Fringing reef, different areas and substrates	Abundance, foraging activity	Four species mainly on sand, *P. multifasciatus* and *P. cyclostomus* on hard bottoms; ontogenetic habitat shifts in *P. multifasicatus*	McCormick (1995)
Mullus barbatus, M. surmuletus	Western Mediterranean	Mud, sand and hard bottoms, depth	Occurrence, abundance, size	*M. barbatus* on muddy bottoms and deeper, *M. surmuletus* more on rough bottoms and shallower	Lombarte et al. (2000)
Mullus barbatus	Eastern Mediterranean	Depth	Abundance, weight, size	Ontogenetic shift from shallower, warmer waters to deeper areas with onset of maturity	Machias & Labropoulou (2002)
Mullus barbatus	Eastern Mediterranean	Lagoons with sandy bottoms and seagrass	Abundance based on fishery landings	Restricted occurrence, high abundance	Katselis et al. (2003)
Mullus surmuletus	Northwest Mediterranean	Seagrass beds	Abundance	High abundance of juveniles	Garcia-Rubies & Macpherson (1995)
Parupeneus barberinus, P. rubescens	Western Indian Ocean	Seagreass bays adjacent to coral reef	Abundance	High abundance of juveniles	Dorenbosch et al. (2006)
Parupeneus barberinoides, P. barberinus, P. ciliatus	Northwest Pacific	Seagrass beds adjacent to coral reef	Abundance, size	High abundance of juveniles	Nakamura & Sano (2003, 2004)
Parupeneus forsskali	Northern Red Sea	Sand and hard bottoms around coral reefs	Abundance, size, foraging behaviour	Large adults and juveniles mainly on sand, intermediate size classes more on hard bottoms	Uiblein (1991) (Figure 2)
Parupeneus forsskali, P. macronema	Northern Red Sea	Sand bottoms around coral reefs	Abundance, foraging activity, day–night changes	High abundance and sediment resuspension rates during day	Yahel et al. (2002)
Parupeneus forsskali, P. macronema	Northern Red Sea	Coral reef and seagrass beds	Occurrence, abundance	High abundance on coral reefs, juveniles on seagrass beds	Al-Rousan et al. (2005)
Parupeneus indicus, P. rubescens	Western Indian Ocean	Seagrass beds	Abundance, length, weight	High abundance of juveniles	Gullström & Dahlberg (2004)
Upeneichthys lineatus, U. stotti	Southwest Pacific	Depth	Abundance	*U. lineatus* mainly inshore, shallower than *U. stotti*	Platell et al. (1998)
Upeneus japonicus, U. taeniopterus	Western Indian Ocean	Mangrove	Occurrence	Presence of juveniles	Muhando et al. (1998)

Depth-related habitat segregation has also been observed in another species pair, the blue-lined goatfish, *Upeneichthys lineatus*, and *U. stotti* (Platell et al. 1998). There are also species differences in substrate preferences and in the flexibility of using alternative habitat types (McCormick 1995; Krajewski et al. 2006).

Fishing pressure

Goatfish species are relevant to fisheries in many areas worldwide and several species have high economic importance. For instance, in Hawaii, Central Pacific, at least six goatfish species are the target of fisheries (Williams et al. 2006). In the Mediterranean, the red mullet and the striped red mullet have been favourite food fishes at least since the Romans and have been heavily exploited in the last few years (e.g. Caddy 1993; European Commission 2005). Since the increase in abundance of striped red mullet in more northern areas (see also the section on temperature changes), a fisheries has been developing there (e.g. ICES 2006).

Goatfishes have been used as fisheries indicators (Table III), often among other species, both to examine immediate pressure from ongoing fisheries or release from fishing impacts in marine protected areas (MPAs). Fisheries pressure leads to a reduction in goatfish abundance and landings, and a marked decrease in size and weight (Table III). Opposite trends in these parameters are observed with release from fishing pressure, as particularly

Table III. Goatfish species as indicators of fisheries impact.

Species	Study area	Major factor(s)	Parameter(s)	Specific observations	Source
Mulloidichthys vanicolensis	Central Pacific	High fishing pressure	Abundance, weight	Decrease in abundance, biomass, mean weight	Friedlander & DeMartini (2002)
Mullus barbatus, M. surmuletus	Western Mediterranean	Long-term fishing pressure	Catch data from landings (1972–1998)	Declined landings	Pinnegar et al. (2003)
Mullus barbatus	Northeast Mediterranean	Fishing pressure, shelf and slope topography	Abundance, dominance in community	Low abundance at deeper sites, dominant at shallowest depth (<32 m)	Labropoulou & Papaconstantinou (2004), Maravelias & Papaconstantinou (2006)
Mullus surmuletus	Western Mediterranean	Reduced fishing pressure	Abundance, size	Increased size	Ordines et al. (2005)
Mullus surmuletus	Northwest Mediterranean	MPA	Abundance, size	Increased abundance in and outside of MPA	Dufour et al. (1995)
Mullus surmuletus	Northwest Mediterranean	MPA	Abundance	Increased abundance, dominant at deep sites	Claudet et al. (2006)
Mullus surmuletus	Adriatic Sea	MPA	Occurrence, abundance	Abundance increases	Lipej et al. (2003)
Parupeneus ciliatus, P. trifasciatus(*)	South Pacific	MPA	Abundance, weight, size	Abundance(*), weight and size increase	Wantiez et al. (1997)

MPA, marine protected area.

happens in MPAs with additional 'spillover effects' to surrounding areas (Table III). Important variables that have to be considered when planning MPAs are site fidelity and home-range size, as goatfishes (e.g. the yellowstripe goatfish, *Mulloidichthys flavolineatus,* and the whitesaddle goatfish *Parupeneus porphyreus*) have distinct requirements for daily and seasonal movements (Holland et al. 1993; Meyer et al. 2000). Also, permanent closures to fisheries should be preferred above intermittent, rotational closures (Williams et al. 2006).

Habitat modification

Approximately 20% of the human population live within 30 km of the sea (Cohen et al. 1997; Gommes et al. 1998), exerting considerable direct or indirect influences on coastal habitats, which add to more

Table IV. Goatfish species as indicators of habitat modification.

Species	Study area	Major factor(s)	Parameter(s)	Specific observations	Source
Mulloidichthys flavolineatus, Parupeneus forsskali	Northern Red Sea	Artificial reef	Abundance	Increased or high abundance	Golani & Diamant (1999), Angel et al. (2002)
Mulloidichthys vanicolensis	Central Pacific	Introduced snapper, *Lutjanus kasmira*	Abundance, length, height above bottom	Increased height above bottom	Schumacher & Parrish (2005)
Mullus surmuletus	Northwest Mediterranean	Invasive alga, *Caulerpa taxifolia*	Abundance, foraging behaviour and movements	Decreased density, foraging budget and search distance	Longepierre et al. (2005)
Parupeneus barberinoides, P. barberinus	Northwest Pacific	Nuclear power plant	Occurrence	No clear effects, one species missing, one newly appearing	Jan et al. (2001)
Parupeneus cyclostomus	Central Pacific	Sedimentation of coral reefs	Abundance	Increased abundance	Tissot (1998)
Parupeneus forsskali	Eastern Mediterranean	Connection to Red Sea by Suez Canal	Occurrence	Isolated single occurrence	Çinar et al. (2006)
Upeneus moluccensis, U. pori	Eastern Mediterranean	Connection to Red Sea by Suez Canal	Distribution, abundance, fisheries landings	Widened distribution, increased abundance and landings	Goren & Galil (2005)

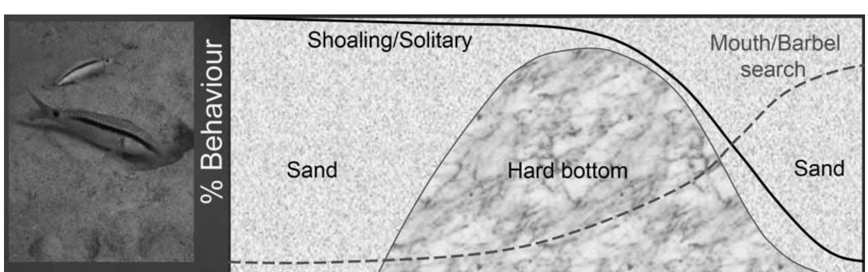
Table V. Goatfish species as indicators of temperature change.

Species	Study area	Major factor(s)	Parameter(s)	Specific observations	Source
Mullus barbatus	Central Mediterranean	Increased sea surface temperature	Abundance, length frequency	Higher recruitment levels	Levi et al. (2003)
Mullus surmuletus	Northeast Atlantic	Increased water and air temperature (1920–1950)	Abundance	Increased abundance	Cushing (1982)
Mullus surmuletus	Northeast Atlantic (English Channel; North Sea)	Increased water temperature, climate change	Abundance	Increased abundance	Vaz et al. (2004), ICES (http://www.ices.dk/marineworld/ices-fishmap.asp)
Upeneus moluccensis	Southeast Mediterranean	Increased water temperature	Catch data from landings	Increased landings	Ben Yami (1955) cited in Goren & Galil (2005)
Upeneus tragula	Southwest Pacific	Increased water temperature	Standard length, age at metamorphosis, barbel morphology	Larger size, earlier metamorphosis	McCormick & Molony (1995)

globally acting impacts, such as climate change. To warrant sustainable use of coastal ecosystems in the future, negative influences have to be monitored and, if necessary, reduced or modified towards long-term ecological integrity.

Goatfishes may to some extent be very useful indicators of human-induced habitat changes other than fisheries, including introduced non-native flora and fauna, pollution, artificial habitat construction, and coastal degradation (Table IV). For instance, the introduction of the non-native common bluestripe snapper, *Lutjanus kasmira* (Forsskål, 1775), in Hawaii has resulted in vertical habitat shift in yellowfin goatfish, *Mulloidichthys vanicolensis*, towards staying more in open water with increased height above the bottom reflecting asymmetrical competition (Schumacher & Parrish 2005). The accidental introduction of the tropical alga *Caulerpa taxifolia* (Vahl 1802) in the Mediterranean resulted in decreased abundance and foraging actvitiy of striped red mullet, *Mullus surmuletus*, with increased algal cover (Longepierre et al. 2005).

Human-made constructions, such as artificial reefs, may lead to increased visits by goatfishes of the respective area and enhance abundance in the immediate surroundings (Golani & Diamant 1999; Angel et al. 2002). Since the Suez canal opened in the 19th century, three goatfish species have immigrated into the Mediterranean from the Red Sea, being so-called Lessepsian migrants (Ben-Tuvia



Size class	I	II	III	IV
Total length (cm)	< 13	13 - 18	18 - 23	> 23
Age (years)	1	2-3	3-5	5-6
Primary search mode	Barbel	Barbel	Barbel	Mouth
Primary habitat	Sand	Hard bottom	Hard bottom	Sand
Shoal association	Monospecific	Mono- and multi-specific	Mono- and multi-specific	Often solitary
Main food	Crustaceans	Fish eggs Crustaceans	Fish eggs Crustaceans	Crustaceans Polychaetes

Figure 2. Red Sea goatfish, *Parupeneus forsskali*, ontogenetic shifts in prey search, resource use, shoaling tendency and association with other species based on a field investigation of four size/age classes in the Gulf of Aqaba, Northern Red Sea (Uiblein 1991). Food selection information is based on Wahbeh & Ajiad (1985).

1966; Table IV). This had consequences for the native red mullet and striped red mullet in the southwestern Mediterranean, which were replaced by two Lessepsian migrants, the goldband goatfish, *Upeneus moluccensis*, and Por's goatfish, *U. pori*, at shallower depths (Golani 1994).

Goatfishes may not always reliably indicate human-induced habitat changes, such as sewage pollution (Guidetti et al. 2003) or there may be no clearly traceable effects, as concluded in a study of fish faunal changes due to the construction of a nuclear power plant (Jan et al. 2001; Table IV).

Temperature and climate change

Water temperature is affected by both climate variation and hydrographical features, including horizontal or vertical movement of water masses. Generally, fishes may respond sensitively to rather minimal changes in water temperatures in various ways, including changes in growth rate, reproductive activity, or development and this is also exemplified by goatfishes (Table V).

Of particular interest is the immigration of goatfishes into previously less frequented or uninhabited areas with increasing temperatures, resulting in increased abundance, fisheries landings, or distributional extension (Table V). Striped red mullet has recently increased in abundance in the English Channel (Vaz et al. 2004) and the North Sea (ICES 2006), including the Norwegian exclusive economic zone (Nedreaas et al. 2006). In the North Sea it was not collected by the international bottom trawl surveys before 1988 and a continuous northwards distributional shift has been demonstrated since, with steadily increasing abundance in the southwestern areas (Beare et al. 2004, http://www.ices.dk/marineworld/fishmap/ices/). This change in distribution and abundance has happened during a phase with demonstrated temperature increase due to global climate change (McCarty et al. 2001; Hulme et al. 2002). Similar findings have recently been documented for several other fish species (Perry et al. 2005).

The northernmost occurrence of striped red mullet, *Mullus surmuletus*, along the Norwegian Sea coast at 60°N has been documented by material caught by local fishermen and deposited in the scientific collections of the Bergen Museum and the Institute of Marine Research (Table VI). The examination of species identity was based on available keys (e.g. Hureau 1986; Quero et al. 2003), additional morphometric and meristic characters, and comparative material (Uiblein, unpublished data). The very first record derives from the island of Stolmen, Austevoll township, in 1943, close to the end of a relatively warm period that lasted from 1920 until 1950 (Southward 1963, 1974; Mason 1976; Cushing 1982). From 1992 onwards, four additional specimens have been collected on various islands southwest of Bergen (Table VI) coinciding with the second, currently ongoing warming period and the increase in abundance of this species in the eastern English Channel and the North Sea (Table V). However, other factors than temperature need to be considered, too, as it would also be required for the recently observed immigration of the West African goatfish, *Pseudupeneus prayensis,* from the Atlantic into the Mediterranean (Mercader 2002).

Goatfishes as key species

The term key species has been used in ecology to rule out those taxa that significantly contribute to the formation and sustaining of community structure and interaction among co-occurring species. The absence of key species would lead to a considerable decline in ecosystem coherence and integrity. Typical key species are those that control communities top-down as predators or bottom-up as important food or prey. Others are so-called ecosystem engineers that may either exert control directly by their simple presence ('autochthonous ecosystem engineers') or indirectly via other abiotic or biotic factors ('allochthonous ecosystem engineers'). Classical examples for the first type are coral reefs and forests and for the second beavers and earthworms.

Table VI. Striped red mullet, *Mullus surmuletus*, collected at 60°N, Norwegian Sea coast, Norway.

No. of individuals	Standard length (mm)	Date	Locality, township	Position	Collector	Method	Collection number
1	240	7 August 1943	Stolmen, Austevoll	59°59′N 05°05′E	N.O. Årland	Gillnet	ZMB 04931
1	254	26 June 1992	Stolmenvågen, Austevoll	59°59′N 05°05′E	R. Njåstad	Eel trap	ZMB 09823
1	256	18 February1993	Gjersvik, Tysnes	60°03′N 05°32′E	S. Sandvik	Gillnet	ZMB 09831
1	94	23 October 1999	Romsa, Kvinneherad	59°40′N 05°44′E	L. Karlsen	Eel trap	ZMB 10816
1	303	30 April 2004	Østre Vinnesvågen, Austevoll	60°01′N 05°16′E	S. Blænes	Gillnet	HIFIRE F5851

ZMB, Bergen Museum fish collection; HIFIRE, Institute of Marine Research fish collection.

Among fishes, several groups have been considered to be allochthonous ecosystem engineers, such as the parrotfishes (Scaridae) that contribute significantly to the sedimentation of coral reefs (Rotjan & Lewis 2005) or the characins (Characidae) that process detritus in streams (Flecker 1996). Goatfishes have hitherto not been sufficiently considered. Due to their very active foraging behaviour with vigorous stirring up of sediments by their barbels and mouths (Randall 1967; Uiblein 1991; McCormick 1995; Krajewski et al. 2006; Figure 1), goatfishes may provide important ecosystem services, including resuspension and the formation of mixed-species foraging associations. These and additional characteristics of their resource use may render goatfishes essential components of food webs in sand-associated coastal ecosystems.

Resuspension

Many littoral hard bottoms undergo a continuous erosion process due to wave action and diverse mining or scraping organisms that contribute to sedimentation and the formation of sandy areas in the immediate surroundings. This is particularly evident on coral reefs, which are usually surrounded by sand habitats in the back- and fore-reef areas, as well as in reef canals, crevices and between reef patches. Corals feed themselves on microscopic food organisms that may, to a large extent, derive from currents transporting them towards the reefs, but there may also be a trophic link between sand bottoms and reef-forming corals, one possible mechanism being the looping back of nutrients from bottom sediments into the open water and surrounding areas by resuspension.

The resuspension of bottom sediments can be enhanced by currents or wave action, but also by distinct organisms. Recent evidence suggests that goatfishes are involved in resuspension (Yahel et al. 2002). For instance, each square metre of a reef site off Eilat, northern Red Sea, has been found to be subjected to, on average, 10 s h^{-1} resuspension activity by the Red Sea goatfish, *Parupeneus forsskali*, with plumes being formed up to 1 m above the bottom and being visible 1–2 min afterwards (Yahel et al. 2002). Apart from dislocation of a large amount of sediment during foraging, this should also contribute to nutrient cycling and transport, thus enriching the plankton. This may, however, also have the rather contrasting effect of damage and the clogging of filter feeders due to the increased abundance of relatively large, suspended detritus (Yahel et al. 2002). In both cases, very different but drastic effects on the overall filter feeding assemblage can be expected that would justify regarding goatfishes as allochthonous ecosystem engineers. There may also be important indirect effects on the sediment-dwelling fauna itself (Choat & Kingett 1982) and on other fish species that often follow goatfishes, thus forming mixed-species foraging associations.

Multi-species foraging associations

The formation of multi-species foraging associations (also called mixed-species, heterospecific or interspecific associations or shoals) may arise if food sources occur that can be shared with advantage. The stirring-up of sediments by goatfishes leads to the uplifting of formerly hidden detritus and other organic material into the water column. This activity attracts other species that follow goatfishes and feed on the newly available particles. Goatfishes themselves may profit, because foraging in larger groups reduces the predation risk. Heterogeneous shoaling may also facilitate access to defended resources by swamping the territories of egg-caring reef-dwellers, such as damselfishes (Fishelson et al. 1974).

Quite a number of studies have reported goatfishes being the primary agent of mixed-species formation, i.e. the nuclear species (see Sazima et al. 2006a; Lukoschek & McCormick 2002a and citations therein). One recent study in the tropical West Atlantic found that spotted goatfish, *Pseudupeneus maculatus*, was the nuclear fish that attracted the largest number of follower species among 27 observed reef fish species (Sazima et al. 2006b). Seventeen (68%) of the total of 25 follower species observed in this study were associated with spotted goatfish.

Multi-species feeding associations are not stable and may change significantly among different habitats, but also during life history. In a study of ontogenetic shifts in resource use in Red Sea goatfish, Uiblein (1991) reported a size-/age-related change in foraging behaviour, habitat use, shoaling tendency and multi-species association. Intermediate size classes were more often found on hard substrates and were also more often associated with other species. One advantage for the goatfishes to form mixed-species flocks on a hard substrate would be to gain access to damselfish territories where they may dislodge fish eggs, a favourite food source during this life-history period (Wahbeh & Ajiad 1985; Figure 2).

Role in coastal food webs

Assemblage structure and interaction within an ecosystem can best be characterized and predicted by food web models that consider all possible trophic pathways (Polis & Winemiller 1995; Belgrano et al. 2005; de Ruiter et al. 2005). Food webs also allow the estimation of the number of indirect interactions between organisms of the same or different trophic levels and evaluation of the overall trophic 'connectedness' of a single species within an ecosystem. Although food web models may become rather complex constructions and may lead to uncertainty about causal relationships between distinct species, they are very valuable tools to obtain a measure on a species' importance in an ecosystem. Species at intermediate trophic levels are often involved in a large number of interactions and may – depending on their own behavioural activity – also exert many important direct and indirect influences on other organisms in the same habitat.

Goatfishes have been relatively rarely considered in food web models, especially at the level of single species. This may derive from insufficient information on their feeding biology in the respective habitat, but may also reflect an underestimation of the overall importance of single goatfish species, populations, or even age classes in coastal ecosystems. One recent study, for instance, included the family Mullidae in a diagram on trophic relationships of estuarine fishes off south Portugal, although the investigation was based only on the diet selection of one species, the red mullet *Mullus barbatus* (Sá et al. 2006).

Because of the hitherto known species-specific differences in goatfish foraging behaviour and diet selection [McCormick 1995; Platell et al. 1998; Nakamura et al. 2003; Krajewski et al. 2006; see also Labropoulou & Eleftheriou (1997) and Aguirre & Sánchez (2005) for the often co-occurring red mullet and striped red mullet], it may be preferable to include only those species that have been thoroughly studied in food web models. Apart from species-specific differences, whether goatfishes also undergo ontogenetic shifts in foraging behaviour, diet, and habitat selection during early (McCormick & Molony 1992; McCormick 1995) as well as later life history (Wahbeh & Ajiad 1985; Uiblein 1991; Labropoulou et al. 1997; Lukoschek & McCormick 2002b; Nakamura & Sano 2003) should also be considered in food web models.

There are also more interactions than just those between goatfishes and their prey that deserve consideration in food web models, such as interactions with predators (McCormick & Kerrigan 1996; Cruz-Escalona et al. 2005), cleaners (Sazima et al. 1999), competitors for food or space (Schumacher & Parrish 2005), territory holders (Alwany et al. 2005), or followers (see previous section). Prey may also profit indirectly from foraging goatfishes due to sediment manipulation (Choat & Kingett 1982) and resuspension (see previous section). Moreover, as some goatfish species are more active at night than during the day (Hobson 1974), nocturnal interactions should also be considered.

Diet selection may vary significantly among goatfish populations leading to variation in their trophic levels among habitats (Stergiou & Karpouzi 2002). Hence, it will be preferable to include diet studies on goatfishes in all habitats where food web models will be established, and from different seasons (Caragitsou & Tsimenides 1982). Of particular interest in this respect would be to also consider the effect of goatfishes on ecosystems they invade as non-native species (Golani 1994) and fishing pressure (Badalamenti et al. 2002; Pinnegar et al. 2003). This would also contribute to the integration of human-induced ecosystem changes in food web models.

There are obviously many possibilities still left open in goatfish ecology to better understand their role in ecosystems. At the same time, there is also a pressing need to further advance with systematic and taxonomic studies of this family.

Goatfish systematics and taxonomy

Detailed morphological studies of an organism group are the prerequisite for understanding systematics, ecology and diversity. Still today, most species are described based on morphological characters, although genetics is becoming increasingly important. Knowledge of the shape, structure, and relative size of external and internal body characters facilitates the interpretation of a species' capability to adapt to distinct environmental conditions. Behavioural studies build firmly on morphological characters that allow an animal to sense the environment, move, feed, rest or interact. Species differences in morphology have clear consequences for niche partitioning as have differences among different life-history stages of the same species. In addition, populations or even co-occurring individuals of the same size may differ morphologically from each other. In recent years, genetics has been employed to study the evolutionary background of morphological differentiation and species formation. This also applies to the goatfishes.

The goatfishes are a family characterized by their conspicuous barbels that differ clearly from similar organs of other fish groups (Kim et al. 2001). Barbels have been found to vary considerably in structure, size, and sensory equipment (e.g. Gosline 1984; Uiblein et al. 1998; Lombarte & Aguirre 1997). However, many other morphological traits of goatfishes, such as body size, coloration, head form, otolith form, or the number of countable characters, such as gillrakers, fin rays, or vertebrae, may vary interspecifically (e.g. Lachner 1954; Thomas 1969; Labropoulou & Eleftheriou 1997; Platell et al. 1998; Uiblein et al. 1998; Aguirre & Lombarte 1999; Kim 2002; Randall 2004) or intraspecifically (e.g. Fage 1909; Rosenblatt & Hoese 1968; Aguirre 1997; McCormick 1993, 1995; Mamuris et al. 1998; Uiblein et al. 1998; Mahé et al. 2005; Pothin et al. 2006; Sabatini 2007).

Currently, 66 species of goatfishes are known and in the last 7 years, seven new goatfish species have been described (Table I). Some genera have been proven to be particularly specious, the most diverse being *Parupeneus*, which consists of 27 species (Randall 2004) followed by *Upeneus* with 23 species. Some species of both genera have a rather restricted occurrence, such as *Parupeneus posteli* and *Upeneus mascareinsis*, which are endemic to Reunion Island (Letourneur et al. 2004). No recent revisions of *Upeneus* and the other less specious genera exist. The status of an additional species from the Eastern Pacific, *Mulloidichthys xanthogrammus* (Gilbert, 1892), is unclear (Byung-Jik Kim, pers. comm.) and, hence, it was not included in the present list (Table I). From future revisions, more detailed systematic information can be obtained and from further exploration of remote areas, like isolated islands, new discoveries of goatfish species can be expected.

All descriptions of goatfish species so far have been based exclusively on morphological data. Genetic studies using various methods have largely confirmed the conclusions from 'classical' systematics (e.g. Shaklee et al. 1982; Stepien et al. 1994; Golani & Ritte 1999; Mamuris et al. 1999; Apostolidis et al. 2001). In some cases, morphological variation may be higher than differentiation found at the genetic level (Stepien et al. 1994). Even among populations from neighbouring or close-by habitats considerable morphological variation exists (Mamuris et al. 1998; Uiblein et al. 1998), which may, to some extent, reflect phenotypic plasticity.

Much more information may still be hidden behind morphological differentiation, as recently discussed by Nielsen (2000) based on a specimen of *Mullus* from the Skagerrak that shows a head shape intermediate between red mullet, *M. barbatus*, and striped red mullet, *M. surmuletus*. A similar observation was previously reported by Fage (1909), who distinguished a southern and a northern form of striped red mullet based mainly on head shape. There have also been problems correctly identifying *Mullus* species during regular bottom trawls in the North Sea (e.g. ICES 2007). Additional confusion may arise, too, from the partly ongoing use of the common name 'red mullet' for both species. Recently, a detailed comparison of *Mullus* specimens from the North Sea with material of *M. barbatus* and *M. surmuletus* from other areas including the two subspecies of red mullet, *M. barbatus barbatus* Linneus, 1758 and *M. b. ponticus* Essipov, 1927, has been started as part of an intended revision of the genus (Byung-Jik Kim & Franz Uiblein).

Conclusions

Many knowledge gaps still exist in goatfish ecology and systematics. However, the currently available data suggest that goatfishes may indeed be suitable habitat indicators and may also qualify as key species in coastal sand-associated ecosystems. Because of considerable inter- and intraspecific variations in habitat preferences, food selection, behaviour, and body structure, special attention should be paid to treat species, populations, and size classes separately from each other. Because not all goatfish species are equally well known and even some new ones may be encountered, exploration, monitoring, and management focusing on this group should be co-ordinated worldwide, thus enhancing information exchange and initiating joint research efforts in goatfish ecology and systematics. At the same time, this study may also serve as a model for screening other organism groups for their potential as ecosystem indicators.

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